

## Parallel structure among environmental gradients and three trophic levels in a subarctic estuary

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### Abstract

We assessed spatial and temporal variability in the physical environment of a subarctic estuary, and examined concurrent patterns of chlorophyll *a* abundance (fluorescence), and zooplankton and forage fish community structure. Surveys were conducted in lower Cook Inlet, Alaska, during late July and early August from 1997 through 1999. Principle components analysis (PCA) revealed that spatial heterogeneity in the physical oceanographic environment of lower Cook Inlet could be modeled as three marine-estuarine gradients characterized by temperature, salinity, bottom depth, and turbidity. The gradients persisted from 1997 through 1999, and PCA explained 68% to 92% of the variance in physical oceanography for each gradient–year combination. Correlations between chlorophyll *a* abundance and distribution and the PCA axes were weak. Chlorophyll was reduced by turbidity, and low levels occurred in areas with high levels of suspended sediments. Detrended correspondence analysis (DCA) was used to order the sample sites based on species composition and to order the zooplankton and forage fish taxa based on similarities among sample sites for each gradient–year. Correlations between the structure of the physical environment (PCA axis 1) and zooplankton community structure (DCA axis 1) were strong ( $r = 0.43$ – $0.86$ ) in all years for the three marine-estuarine gradients, suggesting that zooplankton community composition was structured by the physical environment. The physical environment (PCA) and forage fish community structure (DCA) were weakly correlated in all years along Gradient 2, defined by halocline intensity and surface temperature and salinity, even though these physical variables were more important for defining zooplankton habitats. However, the physical environment (PCA) and forage fish community structure (DCA) were

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strongly correlated along the primary marine-estuarine gradient (#1) in 1997 ( $r=0.87$ ) and 1998 ( $r=0.82$ ). The correlation was poor ( $r=0.32$ ) in 1999, when fish community structure changed markedly in lower Cook Inlet. Capelin (*Mallotus villosus*), walleye pollock (*Theragra chalcogramma*), and arrowtooth flounder (*Atheresthes stomias*) were caught farther north than in previous years. Waters were significantly colder and more saline in 1999, a La Niña year, than in other years of the study. Interannual fluctuations in environmental conditions in lower Cook Inlet did not have substantial effects on zooplankton community structure, although abundance of individual taxa varied significantly. The abundance and distribution of chlorophyll  $\alpha$ , zooplankton and forage fish were affected much more by spatial variability in physical oceanography than by interannual variability. Our examination of physical-biological linkages in lower Cook Inlet supports the concept of “bottom-up control,” i.e., that variability in the physical environment structures higher trophic-level communities by influencing their distribution and abundance across space.

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## 1. Introduction

Marine systems are influenced by physical forcing, which can structure biological communities and often shapes their ecology from the “bottom up.” Correlations are commonly found between physical factors such as temperature and individual ecosystem components, including phytoplankton (Li, Smith, & Platt, 1984; Townsend, Cammen, Holligan, Campbell, & Pettigrew, 1994), zooplankton (Roemmich & McGowan, 1995), fish (Anderson & Piatt, 1999; Castillo, Barbieri, & Gonzalez, 1996; Swartzman, Huang, & Kaluzny, 1992), and seabirds (Ainley, Sydeman, & Norton, 1995; Springer, Rose, & Murphy, 1984). Weather may affect primary production via its influence on physical processes such as upwelling, mixing, and stratification (e.g., Parsons, Takahashi, & Hargrave, 1984; Pingree, 1978; Sambrotto & Lorenzen, 1986). Fewer studies have shown how organisms at multiple trophic levels respond to physical parameters, or have documented the response of one trophic level to another through multiple levels (e.g., Decker, Hunt, & Byrd, 1995; Durant, Anker-Nilssen, & Stenseth, 2003; Gargett, 1997; Hunt & Stabeno, 2002). In most cases, the means by which physical factors evoke a biological response cannot be established, even when correlations are strong (e.g., Committee on the Bering Sea Ecosystem, 1996; Greene, Pershing, Kenney, & Jossi, 2003; Springer et al., 2003). As an example, Aebischer, Coulson, and Colebrook (1990) correlated North Sea weather and four trophic levels, but could not determine the mechanisms and suggested that biological responses were likely a result of more than just trophic interactions or climate forcing.

“Top-down” forcing can also structure community patterns. Worm and Myers (2003) found that eight out of nine regions in the North Atlantic showed inverse correlations of Atlantic cod (*Gadus morhua*) and northern shrimp (*Pandalus borealis*) biomass, suggesting “top-down” control of shrimp populations. In the Black Sea, predatory jellyfish are keystone predators whose presence or absence has a marked influence on community structure (Kideys, 2002). In general, however, data sets that include time series of multiple trophic levels within and among years are difficult to collect, so such analyses are rare. Although effects of one trophic level on another can be difficult to quantify, both direct and indirect trophic interactions can have similarly wide-spread and important ecological consequences (e.g., Shiimoto, Tadokoro, Nagasawa, & Ishida, 1997).

In Alaska, the relative importance of “bottom-up” and “top-down” control mechanisms is paramount to understanding long-term changes in marine ecosystems and the impacts of human activities. For example, the *Exxon Valdez* oil spill in 1989 killed many seabirds and marine mammals (e.g., Monson, Doak, Ballachey, Johnson, & Bodkin, 2000; Piatt & Ford, 1996), but pre-spill changes in ocean climate and forage fish abundance may have had far greater “bottom-up” influences on predator populations (Anderson & Piatt, 1999; Hare & Mantua, 2000; Hollowed, Hare, & Wooster, 2001; Piatt & Anderson, 1996). Similarly, it

remains unclear to what degree the crash of Steller sea lion populations in western Alaska is due to “bottom-up” changes of their food supply (Merrick, Chumbley, & Byrd, 1997), “top-down” predation by killer whales (Estes, Tinker, Williams, & Doak, 1998) and/or competition from other large vertebrates (including humans via fisheries; Shima, Hollowed, & VanBlaricom, 2000).

For this study, we investigated the effects of environmental variability on phytoplankton standing stocks, zooplankton and forage fish communities in lower Cook Inlet, Alaska. One of the main reasons for conducting this study was to examine how seabird populations in lower Cook Inlet are regulated. Are they controlled largely by “bottom-up” forcing? If food regulates seabirds (Piatt & Anderson, 1996), then what regulates their food? How much of the variability in higher trophic levels can be attributed to physical forcing? We used multivariate classification and ordination to describe the spatial and interannual patterns of the physical environment, phytoplankton standing stocks, and zooplankton and forage fish communities in lower Cook Inlet. We identified the physical and biological gradients along which the zooplankton and forage fish communities are structured, and answered the questions: How well do the environmental variables that we measured explain the zooplankton and forage fish community structures? Which variables are most important for explaining the patterns of community structure? And finally, do the apparent physical-biological linkages in lower Cook Inlet support the concept of “bottom-up” control?

## 2. Methods

### 2.1. Study site

Little has been published on the oceanography of Cook Inlet. Most of the available information comes from studies conducted in the 1970s (e.g., Burbank, 1977; Larrance, Tennant, Chester, & Ruffio, 1977; Sharma & Burrell, 1970). More recent sources of information are from projects related to this study (e.g., Abookire, Piatt, & Robards, 2000; Piatt et al., 1999; Speckman, 2004), but there have been no long-term or continuous physical observations at depth in this important estuary.

Cook Inlet is a tidal estuary, exchanging waters at its mouth with the Gulf of Alaska (Fig. 1). Waters from the Alaska Coastal Current, which is a geostrophic, buoyancy-driven flow generated by freshwater input and winds (Royer, 1981), are upwelled as they enter the shallow estuary. These mixed waters, pushing northward into the inlet along the eastern side, are colder and more saline than the fresher, warmer, sediment-laden waters that flow southward along the western shore and exit through Stevenson Entrance into Shelikof Strait (Burbank, 1977; Robards, Rose, & Piatt, 2002). Freshwater input to Cook Inlet comes from snowmelt and rivers, many of which are glacially fed and carry high sediment loads. Additional sediment is carried into the lower inlet from the Copper River via the Alaska Coastal Current (Schumacher & Reed, 1980). The mean tide range in the lower part of the inlet is about 6 m near the town of Homer. Currents are strong and tidally periodic, with average velocities ranging from 3 to 6 knots (Sharma & Burrell, 1970).

### 2.2. Data collection

Data were collected during 3-week cruises in late July and early August from 1997 to 1999. All cruises were part of the Cook Inlet Seabird and Forage Fish Study (Piatt, 2002). In all years, we conducted hydroacoustic and mid-water trawl surveys for forage fishes, and sampled biological and physical oceanographic properties at the end of each trawl. Survey effort centered around three study areas, each associated with a seabird colony, along a north-south axis: Chisik Island in Tuxedni Bay; Gull Island in Kachemak Bay; and northeast of the Barren Islands (Fig. 1). The Barren Islands lie about 200 km northwest of the shelf edge.

Our primary survey platform was the R/V *Pandalus*, a 22 m stern trawler operated by the Alaska Department of Fish and Game. In all years, surveys in some shallow, nearshore areas were conducted from

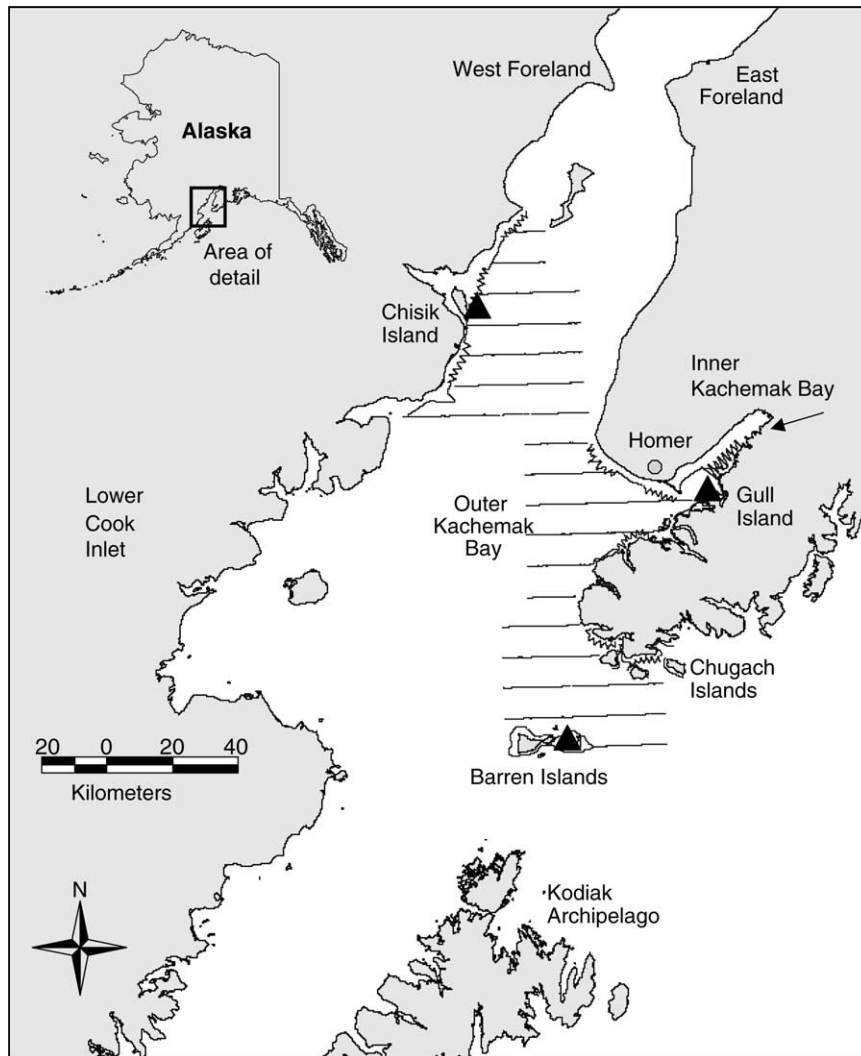


Fig. 1. Transects surveyed in nearshore (zig-zags) and offshore areas in lower Cook Inlet, Alaska, during 1997–1999. Seabird colonies indicated by solid triangles.

the R/V *David Grey*, an 11 m Uniflite cabin cruiser operated by the US Geological Survey. All sampling took place during daylight hours: 0900–2100 Alaska Daylight Time.

Transects were located in both “nearshore” and “offshore” habitats (Fig. 1). Nearshore transects were zig-zag tracks and followed the bathymetry of mainland or island shorelines, where waters were generally deeper than 10 m. Offshore transects cut across open water from one shore to another, over depths ranging from 10 m to greater than 200 m. Transects surveyed from 1997 to 1999 were repeated in all years with the exception of the most northern nearshore transect, which was not surveyed in 1997.

Forage fish were detected using a single beam 120 kHz BioSonics DT4000 hydroacoustic system. Significant aggregations of forage fish were sampled with a modified herring midwater trawl about once per transect. The net had a mouth opening of 50 m<sup>2</sup>, and mesh sizes that decreased from 5 cm in the wings to 1 cm at the cod-end, which was lined with 3 mm mesh. Ground speed was approximately 4–5 km h<sup>−1</sup>

( $2.5 \text{ nm h}^{-1}$ ) during trawling operations. Captured fish were identified to the lowest possible taxon. Fork length was measured for at least 50 individuals of each taxon from each tow. Squid were included as forage fish because they are an important prey item for many marine predators, including seabirds (e.g., Piatt & Kitaysky, 2002). Catch-per-unit-effort (CPUE) of forage fish was standardized to number captured per km trawled. We tried to sample as many transects as possible in each year, but our sampling protocol called for trawling only in areas with much higher than average acoustic backscatter.

At the end of each trawl, a zooplankton sample was collected and a vertical profile of the water column was taken with a CTD (Conductivity-Temperature-Depth) probe (Seabird Electronics Inc., SBE 19 SEACAT). The CTD was lowered from about 2 m to within 1–5 m of the bottom or to a maximum depth of 100 m. In 1998 and 1999, the CTD was fitted with additional sensors to measure fluorescence (WET Labs WETStar) as a proxy for the concentration of chlorophyll  $\alpha$ , and turbidity (D&A Instrument Co.). Fluorescence measurements were not calibrated against extracted chlorophyll  $\alpha$ , and therefore should be interpreted as a relative index. It is not known to what extent measures of fluorescence are affected by turbidity in the water column, although effects are expected to be small (I. Walsh, WET Labs, Inc., pers. comm.). The turbidity meter measured light scattering in a water sample using infrared light of 875 nm (nephelometric turbidity units or NTU). Suspended particles, phytoplankton, bacteria, and dissolved organic matter all contribute to this value.

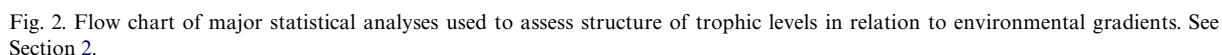
Zooplankton samples were collected with a 3 m long plankton net with a mouth area of  $0.28 \text{ m}^2$  and  $333 \mu\text{m}$  mesh. This mesh size underestimates smaller zooplankton size fractions, such as the early life stages of calanoid copepods, but this bias was consistent throughout all surveys. The weighted net was lowered to within 1–5 m of the bottom or to a maximum depth of 50 m, and then retrieved vertically through the water column. Samples were fixed in 4–6% formalin buffered with seawater. The abundance of all mesozooplankton was determined by sub-sampling in triplicate using a 5 ml Henson–Stempel Pipette (Harris, Wiebe, Lenz, Skjoldal, & Huntley, 2000). Aliquots ranged between 1/100 of the sample and the entire sample, depending on zooplankton density. All samples contained at least 200 animals. Zooplankton were identified to the lowest taxonomic group possible, ranging from phylum to species (38 categories; Appendix I), and to stage when possible. Taxonomy follows the Integrated Taxonomic Information System on-line database (<http://www.itis.usda.gov>). Juveniles of *Acartia*, *Eurytemora*, and *Pseudocalanus* could not be separated beyond genus. Rather than combining unidentified juveniles and adults, juveniles were grouped by genus, resulting in 41 taxonomic groups (Appendix I). To calculate abundance, all stages and sexes were summed for each species or taxonomic group and expressed as number of individuals  $\text{m}^{-3}$  of water sampled. To calculate biomass, wet weights for each taxon (R.T. Cooney, unpublished data) were summed and expressed as  $\text{g m}^{-3}$  or  $\text{g m}^{-2}$ .

### 2.3. Numerical analysis

Major analyses are outlined in a flow chart (Fig. 2). Principle components analysis (PCA) was used to reduce the large number of inter-related variables to a few axes summarizing most of the variability. Detrended correspondence analysis (DCA) was used to summarize biological structure of zooplankton and forage fish communities by ordering them based on similarities in their species composition and abundance. Correlation analysis was used to assess coherence between axes, for example, between an axis that described the physical environment and an axis that described a biological community.

#### 2.3.1. Structure of the physical environment

Totals of 20 (1997) and 23 (1998 and 1999) oceanographic variables were measured or calculated (Table 1). Turbidity was not measured in 1997. Oceanographic data were ordinated for each year using principle components analysis (PCA; PC-ORD, 1997). We included correlated multiple measures of some variables as “variable groups” because we did not know a priori which measures would explain the most variability in the physical environment. Before analysis, all physical variables were log transformed to make the variance independent of the mean and remove heteroscedasticity (Sokal & Rohlf, 1995). Variables were



Environmental gradients across the study area were identified by examining PCA plots of axis 1 and 2 scores for each of the three years. A gradient was identified when the pattern of sample sites on a plot indicated that environmental conditions changed along an axis corresponding to a geographic axis across the study area. Each gradient–year combination was then analyzed separately with PCA, as described above, to determine which environmental variables explained the most variability along each gradient for each year. The first two PCA axes determined to be significant by the broken-stick test (Jackson, 1993) were then compared with the original environmental variables using Pearson correlation coefficients. Variables with correlation coefficients ( $r$ ) of 0.70 or greater were considered important (Manly, 1994) for defining a gradient.

To allow spatial and interannual comparisons of oceanographic variables among parts of the study area, we produced clusters of oceanographically similar sampling sites, or subareas, using Euclidean distance and Ward's hierarchic clustering method (R Development Core Team, 2003). This procedure selects groups with minimal distances among members of the group and maximizes the distance among groups (Legendre & Legendre, 1998). For each year, we ran the cluster analysis on the PCA scores from all axes that were significant for that year (broken-stick test, Jackson, 1993), a procedure used by Barrella and Petrere (2003). Turbidity data were not collected in 1997, so only results for 1998 and 1999 are presented. The number of physical oceanographic sampling sites in each subarea-year ranged from 5 to 13 (Table 2).

Multivariate analysis of variance (MANOVA) by the GLM procedure (SPSS, 1999) was used to test for spatial and temporal differences in physical oceanography. Subarea and year were considered fixed factors.

Table 1

List of variables, arranged by groups, used in analyses of the physical environment and primary production

Variable	Definition	Units
Water depth		
Bottom depth		m
Deep structure, below 5 m		
Thermocline intensity, 1 m	Max. <i>T</i> change in 1 m	°C
Thermocline intensity, 5 m	Max. <i>T</i> change in 5 m	°C
Thermocline depth, 1 m	Depth of max. change in <i>T</i> per 1 m	m
Thermocline depth, 5 m	Depth of max. change in <i>T</i> per 5 m	m
Halocline intensity, 1 m	Max. <i>S</i> change in 1 m	PSS
Halocline intensity, 5 m	Max. <i>S</i> change in 5 m	PSS
Halocline depth, 1 m	Depth of max. change in <i>S</i> per 1 m	m
Halocline depth, 5 m	Depth of max. change in <i>S</i> per 5 m	m
Thermocline off bottom	Bottom depth – thermocline depth, 5 m	m
Surface structure, top 5 m		
Stratification, temperature	Maximum <i>T</i> change	°C
Stratification, salinity	Maximum <i>S</i> change	PSS
Temperature structure	Of water column	
Average		°C
Maximum		°C
Minimum		°C
Surface		°C
Salinity structure	Of water column	
Average		PSS
Maximum		PSS
Minimum		PSS
Surface		PSS
Turbidity structure	Of water column	
Average		NTU
Maximum		NTU
Minimum		NTU
Chlorophyll <i>a</i> , as fluorescence	Of water column	
Average		µg/l
Maximum		µg/l
Minimum		µg/l
Average, top 10 m		µg/l
Average, top 20 m		µg/l

The last 8 variables, measurements of turbidity and chlorophyll, were collected only in 1998 and 1999. *T* = temperature; *S* = salinity, PSS = practical salinity scale; NTU = nephelometric turbidity units.

MANOVA procedures are sensitive to highly correlated dependent variables; therefore, we eliminated one variable from each pair with a correlation coefficient greater than 0.77, which allowed us to retain at least one variable from each variable group (Table 1). Environmental variables were log-transformed to equalize variances (Sokal & Rohlf, 1995). The initial analysis included ten physical oceanographic variables measured in all years (1997–1999). A second analysis included three variables that were measured only in 1998 and 1999: average and maximum turbidity, and average chlorophyll *a*. We used Pillai's Trace (*V*) as the test statistic, because it is the most robust to heteroscedasticity of variance (Olson, 1976). A fixed-effect, two-factor ANOVA using the GLM procedure (SPSS, 1999) was used to examine each response variable separately for each analysis (1997–1999 and 1998–1999). The Scheffé multiple-range test was used to find a posteriori differences ( $\alpha = 0.05$ ) among sample means (SPSS, 1999).

Table 2  
Number of samples in each trophic level, by year and subarea

	Environment	Zooplankton	Forage fish
1997			
Chisik	8	8	8
Outer Bay	13	13	13
Barrens	6	6	6
Chugach	8	8	3
Inner Bay	7	7	3
Subtotal	42	42	33
1998			
Chisik	9	9	4
Outer Bay	7	7	8
Barrens	7	7	3
Chugach	6	6	5
Inner Bay	9	9	12
Subtotal	38	38	32
1999			
Chisik	11	11	11
Outer Bay	10	10	7
Barrens	5	5	6
Chugach	6	6	5
Inner Bay	9	9	6
Subtotal	41	41	35
Total	121	121	100

CTD casts measured temperature, conductivity, and depth. Fluorescence and turbidity were measured in 1998 and 1999.

### 2.3.2. Structure of the zooplankton and forage fish communities

Totals of 121 (zooplankton) and 100 (forage fish) sampling sites were analyzed (Table 2). Detrended correspondence analysis (DCA; PC-ORD, 1997) was used to describe the structures of zooplankton and forage fish communities for each gradient–year. DCA is an eigenanalysis ordination technique based on reciprocal averaging (Hill & Gauch, 1980). DCA displays the patterns of covariation in species distributions by ordering the sample sites based on species composition, and ordering the species or taxonomic groups based on similarities among sample sites (Legendre & Legendre, 1998; Peet, Knox, Case, & Allen, 1988; ter Braak & Prentice, 1988). The technique assumes that species respond unimodally to underlying environmental gradients, which is an appropriate model when the range of environmental variation is large (ter Braak & Prentice, 1988). The eigenvalue associated with each axis is proportional to the variance explained in the sample or species dispersion (Jongman, ter Braak, & Van Tongeren, 1995).

Relative abundance matrices for zooplankton (density as numbers  $\text{m}^{-3}$ ) or forage fish (CPUE as numbers  $\text{km}^{-1}$ ) were analyzed by ordination using DCA. Each forage fish or zooplankton sample was assigned to an environmental gradient based on the PCA of the physical environment. Zooplankton and fish densities were fourth-root transformed to downweight the importance of highly abundant species (Field, Clarke, & Warwick, 1982). Species or species groups that were found in less than 5% of the samples for any year were excluded from analyses for that year (Pielou, 1984).

Six zooplankton taxonomic groups were selected, representing the most abundant adult taxa from each subarea. MANOVA by the GLM procedure (SPSS, 1999) was used to test for spatial and temporal differences in their species composition. Subarea and year were considered fixed factors. A separate MANOVA

was used to test for spatial and temporal differences in species composition of six of the most abundant forage fish species.

### 2.3.3. Relating zooplankton and forage fish community structures to the physical environment

Spearman rank correlation was used to assess correspondence between the DCA (zooplankton or forage fish community structure) and PCA (environmental structure) axes for each year and gradient. In addition, DCA scores for sample sites and species were plotted against one another for each gradient and year, to illustrate shifts in zooplankton or fish species composition over the environmental gradients. We assume that abundance in the water column is proportional to the degree of preference for habitat type or ranges of environmental conditions for both zooplankton and fish. Due to lack of turbidity data for 1997 and an anomalously warm year in 1998, we will focus on results from 1999.

The Mantel test for matrix correspondence estimates the association between two independent dissimilarity matrices that describe the same set of samples, such as a matrix of species composition and one of environmental variables (Diniz-Filho & Bini, 1996). It tests whether the association is stronger than one would predict from chance (Sokal & Rohlf, 1995). The cells of dissimilarity matrices are not independent of one another, and therefore standard techniques for determining significance cannot be used. However, the Pearson correlation coefficient can be used to measure the association between matrices when used as a randomization (Monte Carlo) test; it is then called the standardized Mantel statistic,  $r$ , and ranges between  $-1$  and  $1$  (Sokal & Rohlf, 1995). We used 9999 randomizations to test the significance of  $r$ . We conducted 21 Mantel tests, and therefore used a Bonferroni correction of  $\alpha/N$  or  $0.05/21 = 0.0024$  to determine significant associations between matrices.

We used Mantel tests (PC-ORD, 1997) to compare and link the ecological structure of zooplankton and forage fish species composition and abundance, zooplankton total density and biomass, and phytoplankton standing stock (chlorophyll  $\alpha$  levels) with the spatial gradients present in the physical environment, testing whether the multivariate data are cross-correlated as a gradient (Belgrano, Legendre, Dewarumez, & Frontier, 1995). We tested whether the physical environment, zooplankton and forage fish communities, and chlorophyll  $\alpha$  levels are spatially or temporally structured by using model matrices of oceanographic sub-area and year (Diniz-Filho & Bini, 1996; Sokal & Rohlf, 1995). Finally, we used a matrix of pair-wise geographic distances between sample sites to test whether the structures of the physical environment, zooplankton and forage fish communities, and chlorophyll  $\alpha$  levels were more similar when the distances between sample sites were small (Sokal & Rohlf, 1995).

Zooplankton community structure was represented by DCA scores from the first 3 axes of an ordination for 1997–1999. The zooplankton biomass matrix consisted of 4 summary measures: total zooplankton density in numbers  $\text{m}^{-2}$  and numbers  $\text{m}^{-3}$ , and total zooplankton biomass in  $\text{g m}^{-2}$  and  $\text{g m}^{-3}$ . Forage fish community structure was represented by DCA scores from the first 3 axes of an ordination for 1997–1999. The phytoplankton matrix included 5 measures from each station of chlorophyll  $\alpha$  (Table 1). Biotic matrices were transformed using either a fourth-root (zooplankton density, forage fish CPUE, chlorophyll  $\alpha$  levels) or log (zooplankton biomass) transform. Environmental variables were log transformed and standardized. For phytoplankton, zooplankton, and forage fish, distance matrices were produced using Euclidean distance. A true distance matrix of geographic distances among sample sites was created by using latitude and longitude to calculate linear distances, and (Environmental Systems Research Institute Inc., 1999) to measure the shortest over-water distances between all pairs of sample sites. Model matrices for the five subareas detected by the cluster analysis and three years were created using the dummy variables 1 and 0 to indicate the same or different subarea or year for each pair of sampling sites (Diniz-Filho & Bini, 1996; Legendre & Legendre, 1998). The resultant matrices were then examined for correlation using Mantel tests. All Mantel tests used 121 sampling sites, except for tests that included forage fish, in which case both matrices were reduced to 100 sampling sites (one trawl had no associated physical data).

### 3. Results

#### 3.1. Spatial variability in the physical environment: gradients and subareas

A total of 121 sites was sampled during the 3-year study, 42 in 1997, 38 in 1998, and 41 in 1999 (Table 2). Cluster analyses of the PCA scores summarizing the physical oceanographic environment for 1998 and 1999 showed that the study area can be divided into four distinct subareas. Initial clusters were cut at the height of 20. In both 1998 and 1999, conditions at Chugach and Outer Bay were very similar, but because sample sites in these two areas are spatially separated, we grouped them into unique clusters, resulting in five subareas: Chisik, Outer Kachemak Bay (hereafter called “Outer Bay”), the Barrens, Chugach, and Inner Kachemak Bay (Inner Bay; Fig. 3). Cluster analysis for 1997 failed to group neighboring sample sites clearly, likely due to lack of turbidity data, and is therefore not shown. Subareas are useful for interpretation of results and aid in the visualization of patterns in the PCA plots. They also allow statistical testing of differences among parts of the gradients. We found significant effects of space (subarea) on all ten physical oceanographic variables (MANOVA;  $V_{40,400}=2.11$ ,  $p<0.001$ ) and turbidity (MANOVA;  $V_{12,207}=0.86$ ,  $p<0.001$ ). However, tabled values should be interpreted more cautiously than standard  $p$ -values, because the same data were used in the cluster analysis to determine the subareas. MANOVA and ANOVA results are reported in detail in Speckman (2004).

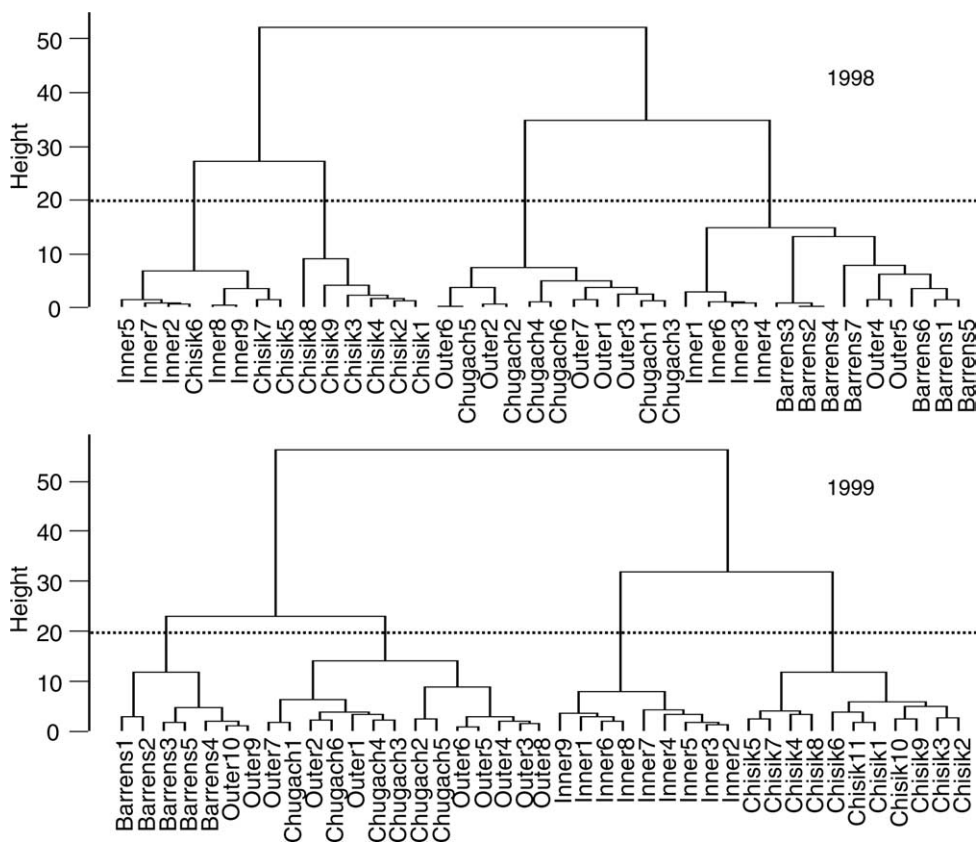


Fig. 3. Ward's hierarchic cluster analysis of the sampling site scores from the principle components analysis (PCA) of the physical environment for 1998 and 1999. Clusters were cut at a height of 20, which divided the study area into five subareas that are oceanographically or spatially distinct: Chisik, Outer (Kachemak) Bay, the Barrens, Chugach, and Inner (Kachemak) Bay. Turbidity data were not collected in 1997, so only data from 1998 (38 sampling sites) and 1999 (41 sampling sites) are presented.

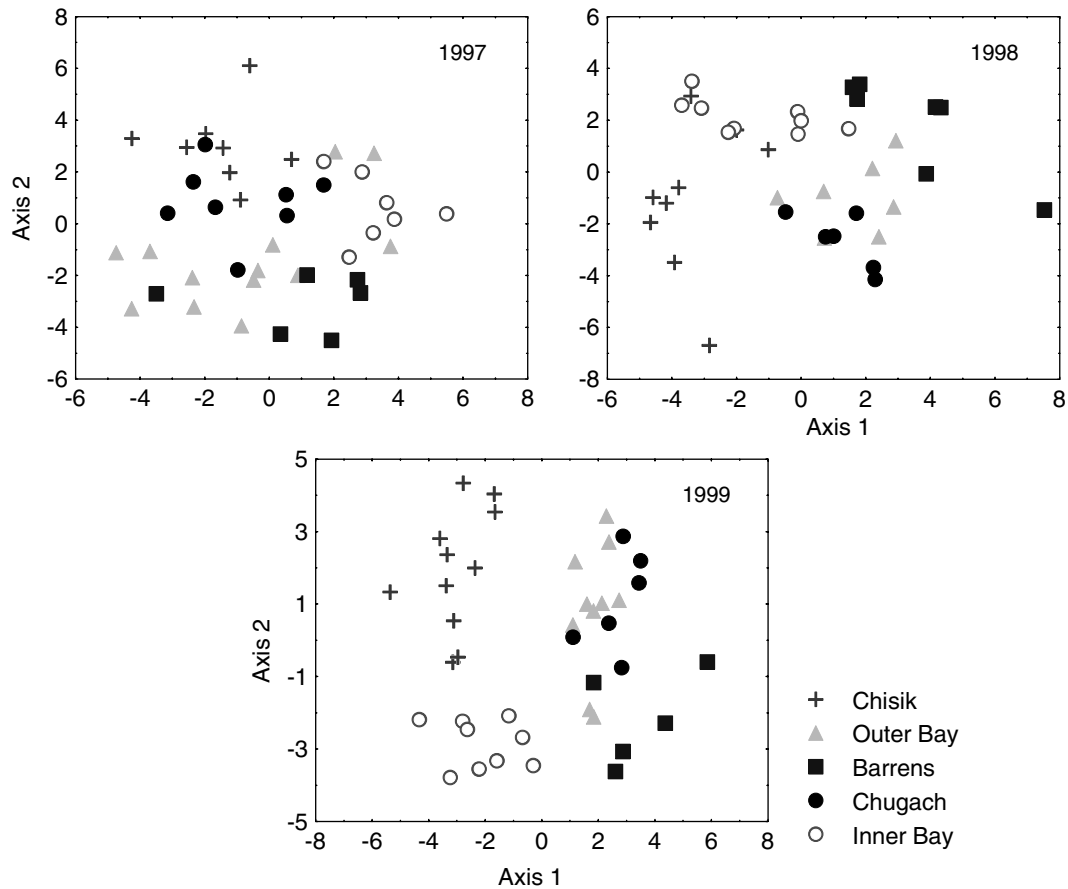


Fig. 4. Scatter plots of first and second axes from principle components analysis (PCA) of the physical oceanographic variables measured at each sampling site during 1997–1999. Symbols indicate values from each of the five subareas derived from cluster analysis. Without turbidity data in 1997, Chisik and Chugach could not be separated.

Scatter plots for each year (Fig. 4) were made using the first and second axes from the same PCA that was used for the cluster analyses. Data from each subarea defined by cluster analysis were coded with unique symbols. These plots show groupings of sites that are similar to those of the cluster analysis. PCA, however, does not force divisions among sites. This analysis, therefore, suggested that the sampling sites are arranged along persistent gradients in the physical oceanographic environment (Fig. 4). The physical gradients correspond to geographic axes across the study area (Fig. 5).

For example, for 1999, we plotted Axis 1 vs. Axis 2 from a PCA analysis (Fig. 5) that used only data from the subareas Chisik, Outer Bay, and the Barrens, all of which lie along Gradient 1. This plot allows one to see more easily how the PCA scores for each subarea, which are summaries of the physical oceanography, are arranged along a geographic line, which is the gradient. This analysis was repeated (Fig. 5) for Gradient 2 (Outer and Inner bays) and Gradient 3 (the Barrens and the Chugach) and for all years.

Each gradient is comprised of 2 or 3 subareas. Use of subareas allows us to statistically differentiate among physical parameters along the gradients. Pearson correlation of the original physical oceanographic variables with the PCA axes for each gradient–year combination indicates which physical variables explain the most variability along each gradient (Table 3). The total variance explained by PCA analysis for each gradient–year ranged from 68% to 92%, and from 17% to 45% for a single PCA axis.

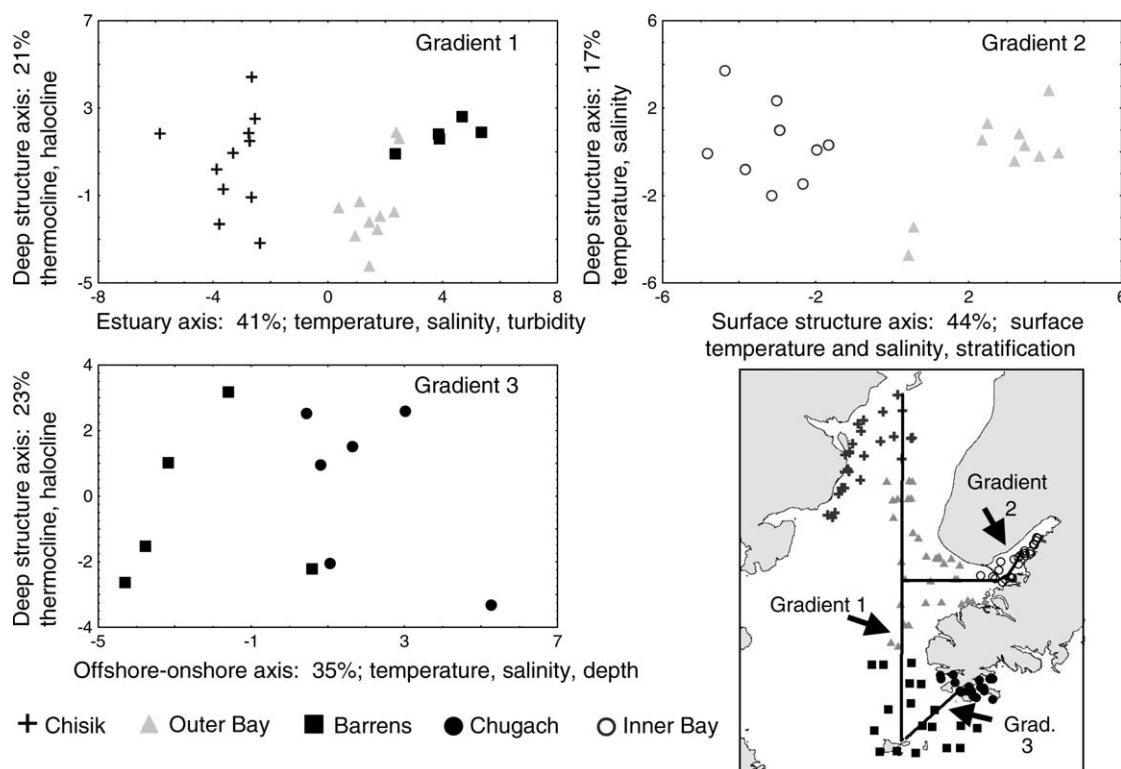


Fig. 5. Scatter plots of first and second axes from principle components analysis (PCA) of the physical oceanographic variables at the sampling sites along each of three gradients. Data shown are for 1999; similar results were observed in other years. For each gradient, the arrangement of sampling sites corresponds to a geographic axis across the study area. Each scatterplot axis is labeled to indicate which physical variables best explain overall variability (with percentage explained). For all 3 gradients, the first axis captures the variability along the gradient (and among subareas), while the second axis captures variability among sample sites.

Gradient 1 extends into the inlet from the southern marine end to the northern estuarine end of the study area (Fig. 5). Waters around the Barren Islands are the deepest of the subareas (>200 m). Cold, salty waters well up near the Barren Islands, resulting in the lowest average temperatures (8.8 °C; Scheffé test,  $p < 0.01$ ) and highest maximum salinities (32.2 PSS; Scheffé test,  $p < 0.01$ ) measured during this study. Surface waters have little stratification, the average thermocline is strong (0.15 °C m<sup>-1</sup>) and deep (28 m), and average turbidity is low (8.1 NTU; Fig. 6). Upwelled waters that are oceanic in character are pushed along the eastern shore of Cook Inlet (Burbank, 1977) and to the north along Gradient 1. These oceanic waters are gradually mixed and diluted as they move northward (Burbank, 1977), becoming warmer and fresher, and forming a transition zone between marine and estuarine waters. Outer Bay is characterized by intermediate average temperatures (9.9 °C) and minimum salinities (30.8 PSS), thermoclines of moderate intensity (0.07 °C m<sup>-1</sup>), intermediate levels of surface stratification (0.7 PSS m<sup>-1</sup>), and low turbidity (8.5 NTU).

Waters continue to become warmer, fresher, and more turbid (Fig. 6) along Gradient 1 toward the north to Chisik Island. The Chisik subarea is characterized by estuarine waters and relatively shallow depths (<60 m). It tends to be well-mixed, but a shallow, weak thermocline can form. Stratification in the top 5 m occurs but is uncommon. The Chisik subarea has the warmest average temperatures (11.6 °C; Scheffé test,  $p < 0.05$ ) and the lowest maximum salinity (29.6 PSS; Scheffé test,  $p < 0.05$ ) of all subareas (Fig. 6). Chisik also has the highest average turbidity levels throughout the water column of any subarea (12.0 NTU; Scheffé

Table 3

Pearson correlations between PCA environmental axes 1 and 2, and measures of the physical environment, for each year and gradient

	GRADIENT 1						GRADIENT 2						GRADIENT 3					
	1997		1998		1999		1997		1998		1999		1997		1998		1999	
Total variance explained, % (number of significant axes)	80.0 (3)		68.1 (2)		85.7 (4)		76.0 (3)		71.3 (3)		74.2 (3)		86.1 (3)		77.8 (3)		92.4 (5)	
Variance explained per axis, % (axis)	36.9 (1)	30.9 (2)	45 (1)	23.1 (2)	40.9 (1)	20.8 (2)	45.4 (1)	19.2 (2)	38.2 (1)	19.6 (2)	44.1 (1)	16.5 (2)	41.3 (1)	31.2 (2)	39.2 (1)	26.1 (2)	34.5 (1)	22.5 (2)
Bottom depth (m)	<b>-0.90</b>	-0.11	0.66	-0.50	0.45	0.64	-0.34	<b>0.77</b>	-0.06	0.52	-0.58	-0.59	<b>-0.92</b>	-0.10	-0.61	-0.58	<b>-0.83</b>	-0.11
Thermocline intensity, 5 m (°C)	-0.23	<b>-0.91</b>	0.36	-0.59	0.22	<b>0.76</b>	<b>0.89</b>	0.16	0.12	-0.29	-0.67	-0.20	-0.67	-0.68	-0.23	<b>-0.80</b>	-0.37	<b>-0.79</b>
Thermocline depth 5 m (m)	-0.68	-0.18	-0.04	<b>-0.86</b>	0.37	0.50	0.01	<b>0.87</b>	-0.84	0.15	-0.18	-0.21	-0.42	-0.09	-0.47	<b>-0.75</b>	-0.10	0.16
Thermocline off bottom (m)	<b>-0.75</b>	-0.06	<b>0.75</b>	0.11	0.33	0.58	-0.38	0.30	0.05	<b>0.78</b>	-0.59	-0.61	<b>-0.85</b>	-0.02	-0.62	0.50	<b>-0.79</b>	0.06
Thermocline intensity, 1 m (°C)	-0.29	<b>-0.91</b>	-0.53	-0.58	0.22	0.69	<b>0.89</b>	0.21	<b>-0.73</b>	0.21	<b>-0.73</b>	-0.12	-0.60	<b>-0.71</b>	-0.26	-0.55	-0.35	<b>-0.85</b>
Thermocline depth 1 m (m)	-0.62	-0.10	<b>-0.80</b>	-0.47	0.36	0.49	-0.08	<b>0.79</b>	<b>-0.75</b>	-0.45	-0.08	-0.14	-0.41	-0.21	0.57	<b>-0.73</b>	0.10	0.25
Stratification, temperature (°C)	-0.20	-0.68	<b>-0.92</b>	0.17	-0.16	0.24	<b>0.86</b>	0.15	0.13	<b>-0.84</b>	<b>-0.86</b>	-0.29	-0.69	-0.36	<b>0.93</b>	0.17	-0.14	-0.54
Temperature, surface (°C)	0.47	<b>-0.75</b>	<b>-0.80</b>	-0.47	<b>-0.90</b>	0.21	<b>0.81</b>	-0.04	<b>-0.75</b>	-0.46	<b>-0.91</b>	0.21	0.23	<b>-0.89</b>	0.57	<b>-0.73</b>	<b>0.75</b>	-0.45
Temperature, average (°C)	<b>0.94</b>	-0.04	<b>-0.83</b>	0.33	<b>-0.95</b>	-0.10	0.06	-0.63	0.43	-0.66	0.44	<b>0.70</b>	<b>0.85</b>	-0.38	<b>0.82</b>	0.44	<b>0.99</b>	-0.03
Temperature, maximum (°C)	0.48	<b>-0.77</b>	-0.22	<b>-0.87</b>	<b>-0.91</b>	0.25	<b>0.83</b>	-0.12	<b>-0.92</b>	0.08	<b>-0.94</b>	0.18	0.21	<b>-0.89</b>	-0.43	<b>-0.76</b>	0.67	-0.46
Temperature, minimum (°C)	<b>0.91</b>	0.23	<b>0.75</b>	0.05	<b>-0.93</b>	-0.24	-0.44	-0.65	0.36	<b>0.70</b>	0.69	0.52	<b>0.89</b>	-0.18	<b>-0.80</b>	0.14	<b>0.93</b>	0.11
Halocline intensity, 1 m (PSS)	-0.16	<b>-0.94</b>	-0.28	<b>-0.89</b>	-0.24	<b>0.74</b>	<b>0.92</b>	0.15	<b>-0.93</b>	-0.05	<b>-0.91</b>	0.06	-0.46	<b>-0.80</b>	-0.29	<b>-0.84</b>	-0.25	<b>-0.90</b>
Halocline depth, 1 m (m)	-0.66	0.09	0.45	-0.11	0.30	0.64	-0.54	0.53	0.45	0.41	0.14	-0.20	-0.65	-0.17	-0.51	-0.08	0.06	0.55
Halocline intensity, 5 m (PSS)	0.00	<b>-0.94</b>	-0.53	-0.58	-0.29	<b>0.79</b>	<b>0.93</b>	0.13	-0.71	0.27	<b>-0.89</b>	0.11	-0.47	<b>-0.83</b>	-0.26	-0.55	-0.47	<b>-0.79</b>
Halocline depth, 5 m (m)	-0.65	-0.01	<b>0.87</b>	0.25	0.46	0.54	-0.43	0.52	<b>0.94</b>	0.05	0.26	-0.37	-0.63	-0.03	<b>-0.82</b>	0.31	0.09	0.51
Stratification, salinity (°C)	-0.18	-0.68	<b>0.91</b>	-0.19	-0.16	0.24	<b>0.85</b>	0.08	<b>0.78</b>	0.43	<b>-0.86</b>	-0.29	<b>-0.70</b>	-0.37	<b>-0.93</b>	-0.20	-0.14	-0.54
Salinity, surface (PSS)	-0.53	0.53	<b>0.89</b>	-0.30	<b>0.86</b>	-0.32	<b>-0.83</b>	-0.13	-0.05	<b>0.73</b>	<b>0.86</b>	-0.36	-0.53	<b>0.77</b>	<b>-0.88</b>	-0.30	<b>-0.83</b>	0.21
Salinity, average (PSS)	<b>-0.87</b>	0.08	<b>0.87</b>	0.23	<b>0.94</b>	-0.19	<b>-0.79</b>	0.37	<b>0.94</b>	0.05	0.64	<b>-0.71</b>	<b>-0.78</b>	0.55	<b>-0.80</b>	0.29	<b>-0.99</b>	0.07
Salinity, maximum (PSS)	<b>-0.77</b>	-0.05	<b>-0.74</b>	0.48	<b>0.92</b>	0.01	-0.24	-0.25	-0.60	0.01	0.22	<b>-0.89</b>	<b>-0.76</b>	0.48	-0.38	0.42	<b>-0.94</b>	0.13
Salinity, minimum (PSS)	-0.53	0.55	-0.51	0.58	<b>0.85</b>	-0.34	<b>-0.83</b>	-0.16	-0.65	0.47	<b>0.92</b>	-0.26	-0.52	<b>0.83</b>	<b>-0.71</b>	0.43	-0.66	0.50
Turbidity, average (NTU)	-	-	-0.62	-0.01	<b>-0.87</b>	0.06	-	-	-0.13	-0.13	<b>-0.72</b>	0.50	-	-	0.46	-0.28	-0.28	0.40
Turbidity, maximum (NTU)	-	-	-0.51	0.58	<b>-0.86</b>	0.19	-	-	-0.65	0.47	-0.50	-0.14	-	-	<b>-0.71</b>	0.43	0.07	0.29
Turbidity, minimum (NTU)	-	-	-0.62	-0.01	-0.42	0.21	-	-	-0.13	-0.13	-0.28	0.05	-	-	0.46	-0.28	-0.26	0.40

Correlation coefficients above 0.70 are in bold.

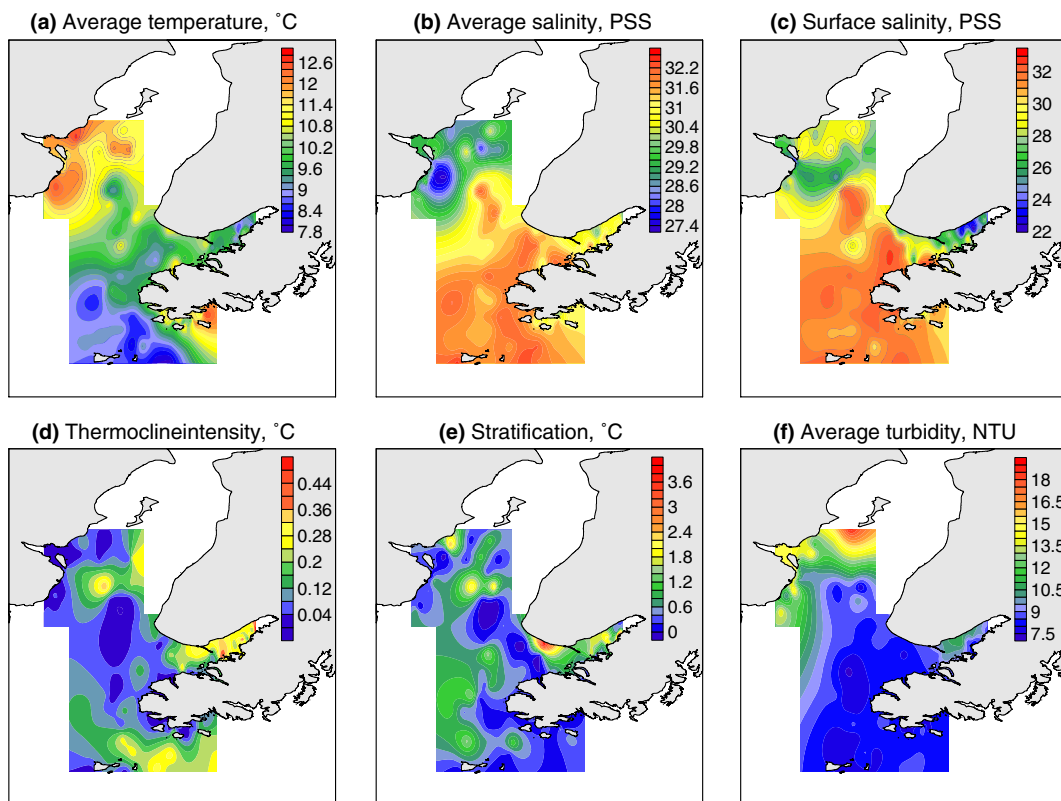


Fig. 6. Spatial variability in the physical environment. Plots are kriged interpolations of selected variables from 121 sampling sites combined over all three years of study.

test,  $p < 0.01$ ). Within the water column, turbidity levels are highest near the sea floor, where strong currents keep sediments suspended (Fig. 7).

Euphausiids, *Oikopleura* spp., and *Calanus marshallae* were present in the Barrens and declined rapidly in abundance towards Outer Bay, whereas *Limacina* spp. and *Oithona* spp. persisted into Outer Bay in low numbers (Fig. 8). *Pseudocalanus minutus*, *Centropages abdominalis*, and *Acartia longiremis* were ubiquitous or nearly so along Gradient 1, although their numbers decreased to the north. Nearshore species such as *Acartia clausi* and *Tortanus discaudatus* were found almost exclusively near Chisik at the northern end of Gradient 1.

In 1997 (Fig. 9) and 1998, capelin (*Mallotus villosus*), North Pacific bobtail squid (*Rossia pacifica*), and pollock (*Theragra chalcogramma*) were present in the Barrens. Pollock extended into Outer Bay in large numbers but were not found at Chisik. Herring (*Clupea pallasii*) and Pacific cod (*Gadus macrocephalus*) were present in Outer Bay and Chisik. Pacific sand lance (*Ammodytes hexapterus*) were abundant in Outer Bay and Chisik but were less common to the south. Many species, including salmon (*Oncorhynchus* spp.), Pacific lamprey (*Lampetra tridentata*), longfin smelt (*Spirinchus thaleichthys*), and Pacific sandfish (*Trichodon trichodon*) were found exclusively at the northern end of Gradient 1, in the Chisik subarea. Patterns of fish distribution were similar in 1998 (not shown), but forage fish community structure changed markedly in 1999. Ordination of sampling sites based on fish species composition in 1999 no longer paralleled the ordination of sampling sites based on physical oceanography, because the northern (Chisik) and middle (Outer Bay) portions of Gradient 1 were reversed (Fig. 10). The switch was caused by the presence of capelin, pollock,

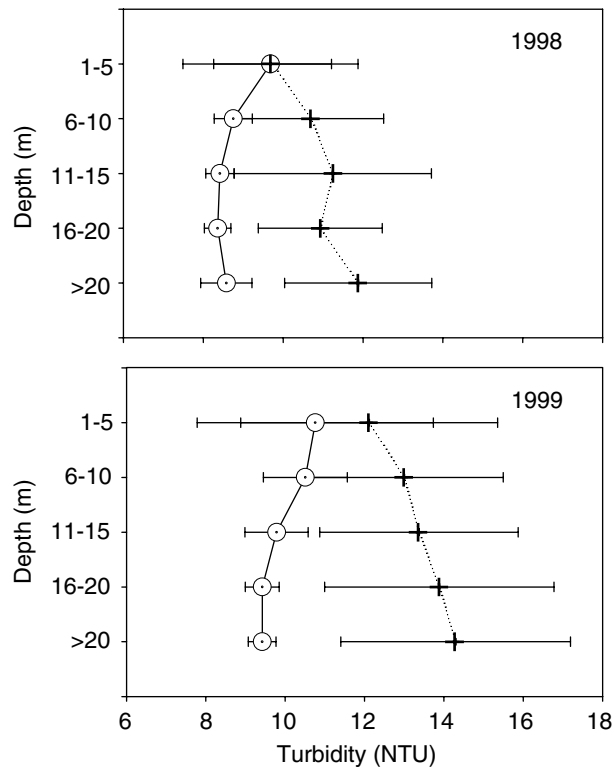


Fig. 7. Average turbidity at Chisik (plus symbols) and Inner Bay (open circles).

and arrowtooth flounder (*Atheresthes stomias*) at Chisik, and lack of or low numbers of those species in Outer Bay. In 1999, Chisik was more similar to the Barrens than to Outer Bay.

Within the larger lower Cook Inlet region, Kachemak Bay branches off to the north-east, and Gradient 2 runs roughly west-east through Outer and Inner Kachemak Bay (Fig. 5, Table 3). Depths in Inner Bay range from shallow shelves to over 90 m. A fjord, Inner Bay is estuarine and highly influenced by glacial run-off. The fresh, turbid glacial outflow does not mix throughout the water column but forms layers on the surface (Fig. 6(c)). Waters in Inner Bay are stratified, with temperatures changing as much as 4 °C and salinities as much as 5 PSS in the top 5 m of the water column. Salinity stratification and halocline intensity in Inner Bay are significantly higher than in other subareas (1.5 PSS, Scheffé test,  $p < 0.01$ ; 0.4 PSS  $m^{-1}$ , Scheffé test,  $p < 0.01$ ), and minimum salinity levels are significantly lower than in other subareas (25.9 PSS; Scheffé test,  $p < 0.01$ ). Although average turbidity levels in Inner Bay are intermediate, most of the suspended sediments that are present are concentrated in the top 5 or 10 m of the water column in the stratified surface layer (Fig. 7). Inner Bay therefore includes many of the sample sites with maximum turbidity levels.

Zooplankton groups that preferred the more mixed, more marine waters of Outer Bay included *Eurytemora herdmani*, ostracods, barnacle nauplii, and Majid crab zoeae (Fig. 11). *Pseudocalanus* spp. juveniles, *P. newmani*, *P. minutus*, and *C. marshallae* increased in abundance into Inner Bay. *Acartia longiremis*, *Oithona* spp., and *C. abdominalis* were abundant throughout Gradient 2. *Acartia clausi*, the most nearshore of the species, occurred almost exclusively in Inner Bay. In all years, ordination of forage fish along Gradient 2 indicated that fish were distributed independently of the physical gradient we defined (Fig. 12).

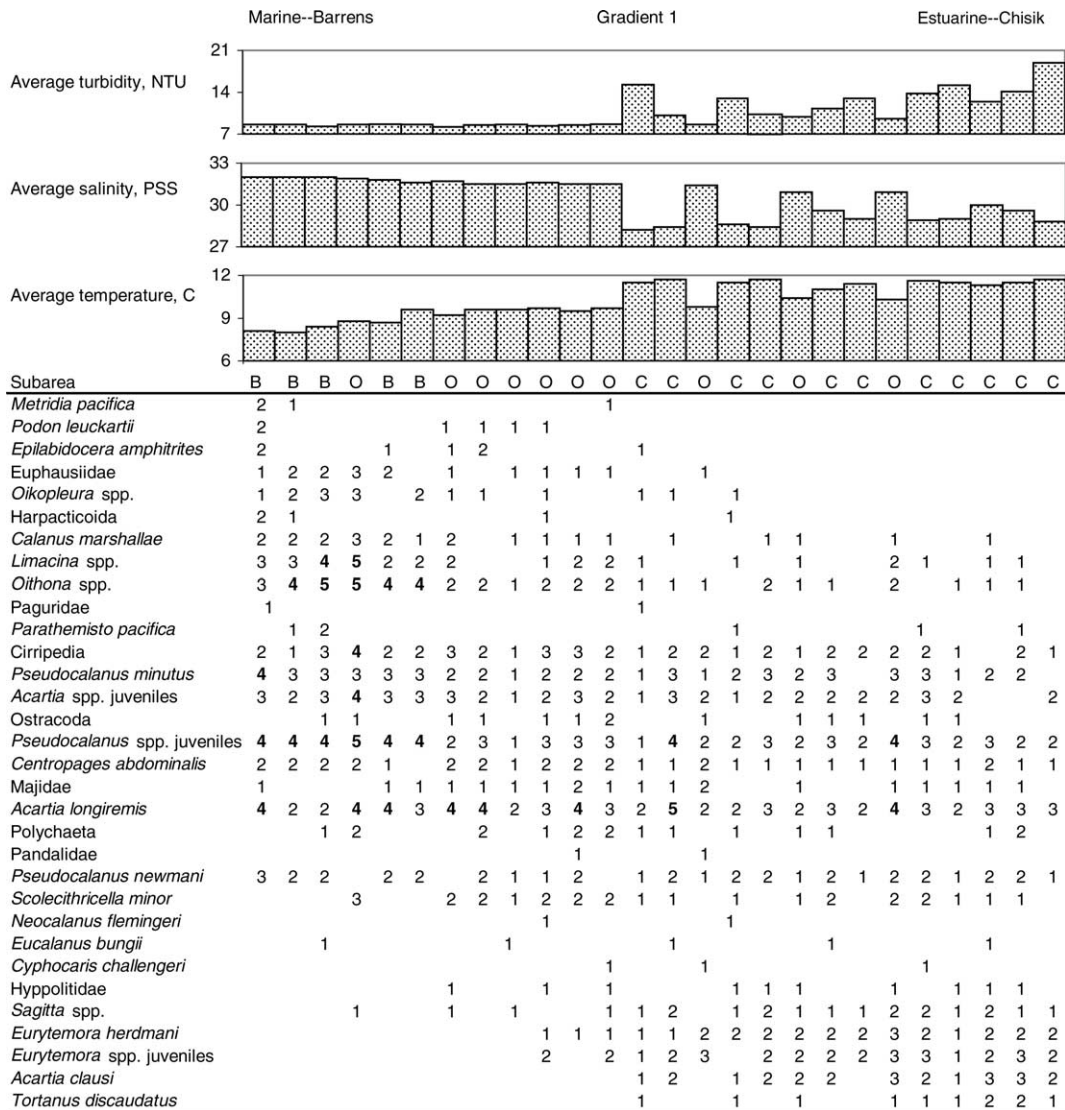
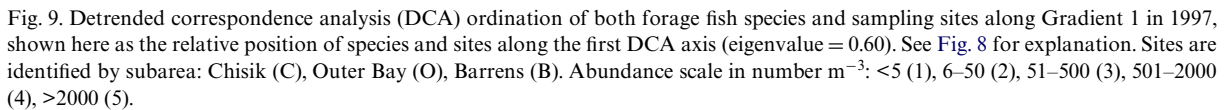


Fig. 8. Detrended correspondence analysis (DCA) ordination of both zooplankton species and sampling sites along Gradient 1 in 1999 (see Fig. 5), shown here as the relative position of species and sites along the first DCA axis (eigenvalue = 0.22). Physical oceanographic variables from three different parameter groups (i.e., turbidity, temperature, salinity) that were most highly correlated with PCA axis 1 indicate (upper 3 panels) the dominant components of the environmental gradient along which species composition changes (lower panel, list of species). Sites are identified by subarea: Chisik (C), Outer Bay (O), Barrens (B). Abundances >200 are in bold. Abundance scale in number  $m^{-3}$ : <5 (1), 6–50 (2), 51–200 (3), 201–500 (4), >500 (5).

Gradient 3 extends from the Barren Islands to the nearshore environment of the Chugach Islands (Fig. 5, Table 3). The Chugach subarea is coastal and glacially influenced, like Inner Bay, but because of its exposure to winds and currents, Chugach is oceanographically more similar to Outer Bay (Fig. 3), serving as a transition zone between marine waters and more estuarine waters in nearby sheltered fjords. Depths in Chugach are <60 m, rapidly dropping to just over 200 m near the Barrens. Average temperatures at Chugach are significantly warmer than Outer Bay, Inner Bay or the Barrens, and significantly cooler than Chisik



*Calanus marshallae*, *Limacina* spp., and *Oithona* spp. were common at the Barrens and declined in abundance towards the Chugach subarea (Fig. 13). *Acartia longiremis*, *P. newmani*, *P. minutus*, and Cirripedia were common throughout Gradient 3. *Scolecithricella minor* and many other groups were rare in the Chugach. Very low densities of several oceanic species (Ozaki & Minoda, 1996), including *Eucalanus bungii*, *Metridia pacifica*, and *Neocalanus flemingeri*, were found in the Barrens, Chugach, and Outer Bay, likely transported by upwelled oceanic waters onto the continental shelf. Along Gradient 3, forage fish were divided into two distinct communities: capelin and pollock were found at the Barrens, and herring and sand lance were found at Chugach (Fig. 14).

Our study spanned a 3-year period of significant atmospheric events, which included both the 1997–1998 El Niño and the following 1999 La Niña. We found significant effects of year on five physical oceanographic

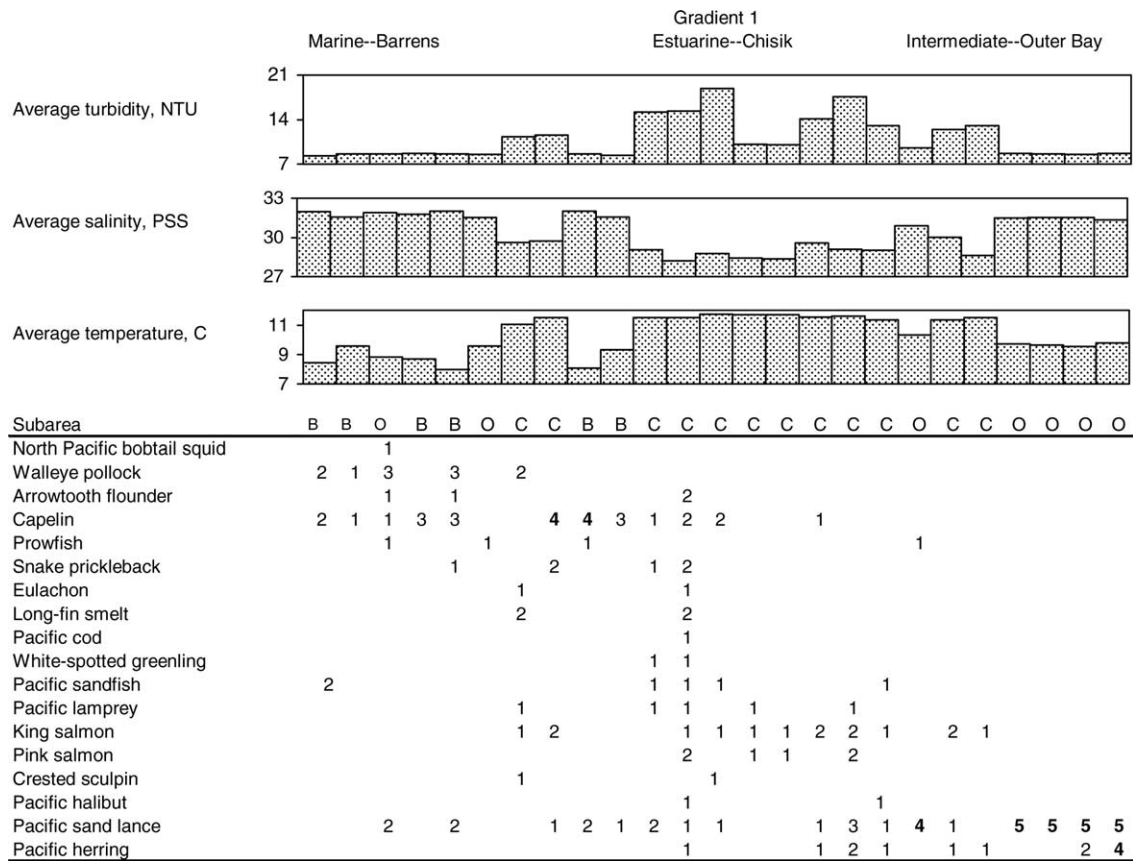


Fig. 10. Detrended correspondence analysis (DCA) ordination of both forage fish species and sampling sites along Gradient 1 in 1999, shown here as the relative position of species and sites along the first DCA axis (eigenvalue = 0.62). See Fig. 8 for explanation. Sites are identified by subarea: Chisik (C), Outer Bay (O), Barrens (B). Abundance scale in number  $m^{-3}$ : <5 (1), 6–50 (2), 51–500 (3), 501–2000 (4), >2000 (5).

variables (average and maximum temperature, maximum and minimum salinity, and intensity of salinity stratification; MANOVA;  $V_{20,196} = 0.88$ ,  $p < 0.001$ ) and turbidity (MANOVA;  $V_{3,67} = 0.30$ ,  $p < 0.001$ ). Again, tabled values should be interpreted cautiously because the same data were used in the cluster analysis to determine the subareas. As the El Niño developed, Chugach and the Barrens, the two subareas most closely linked to Gulf of Alaska waters, exhibited increased maximum temperatures relative to the other two years of the study. The three subareas that are more estuarine in location, Chisik, Outer Bay, and Inner Bay, did not exhibit increased temperatures until 1998, when the average temperature across the study area increased significantly from 1997 (Scheffé test,  $p < 0.05$ ; Fig. 15(a)). Temperatures dropped in 1999, when average and maximum temperatures were significantly lower than in 1998 (for both, Scheffé test,  $p < 0.01$ ), and maximum temperature was significantly lower than in 1997 (Scheffé test,  $p < 0.01$ ; Fig. 15(b)). Minimum salinity was lower in 1998 than in 1997 (Scheffé test,  $p < 0.01$ ; Fig. 15(c)). Average turbidity was significantly higher in 1999 than in 1998 (Scheffé test,  $p < 0.01$ ); this pattern was maintained in all subareas (Fig. 15(d)). Overall, average conditions in lower Cook Inlet in 1998 were the warmest and freshest. Measures of temperature in 1998 averaged from 0.5 to 1.1 °C warmer, and measures of salinity averaged from 1 to 2 PSS lower, than in 1997 or 1999.

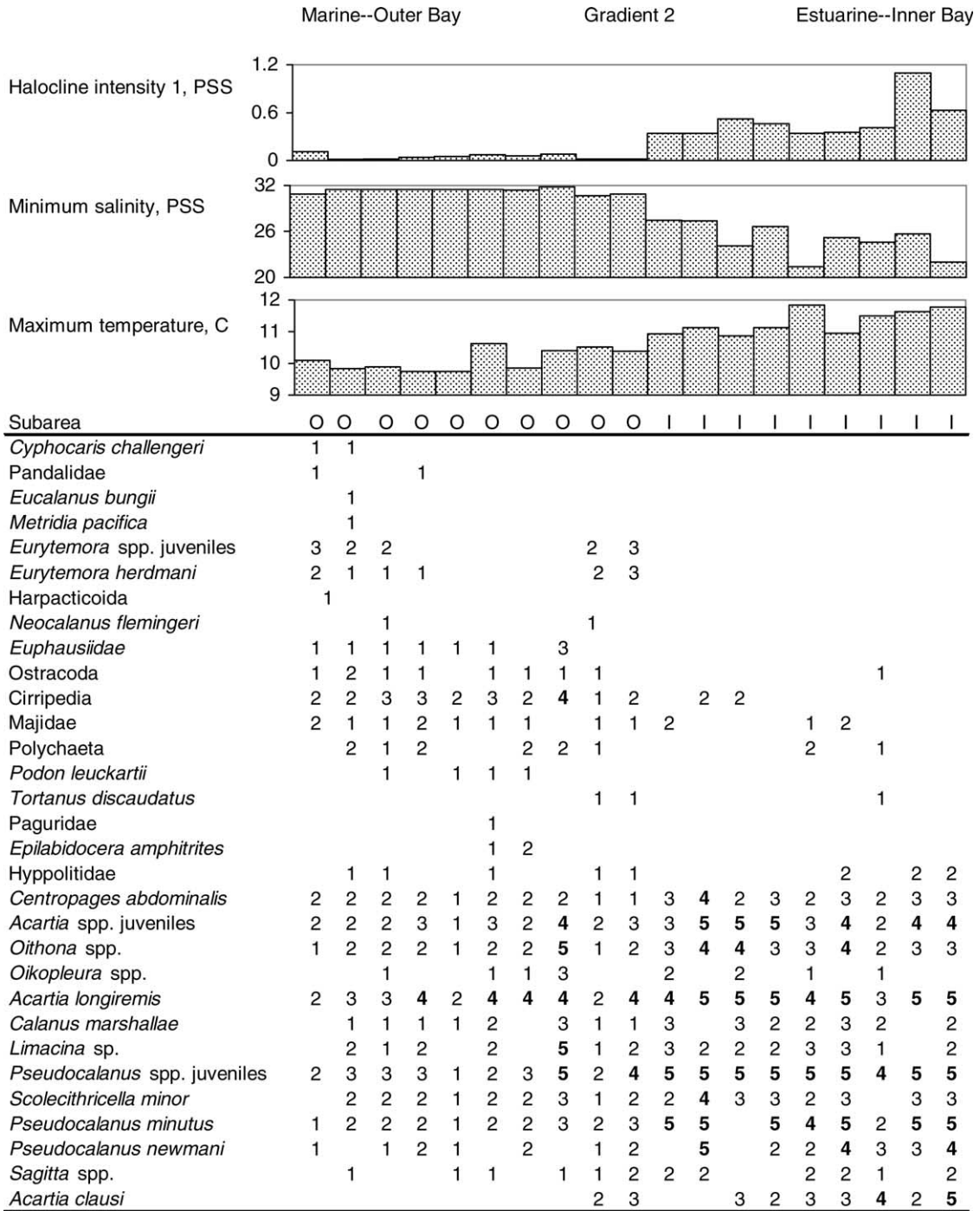


Fig. 11. Detrended correspondence analysis (DCA) ordination of both zooplankton species and sampling sites along Gradient 2 in 1999, shown here as the relative position of species and sites along the first DCA axis (eigenvalue = 0.21). See Fig. 8 for explanation. Sites are identified by subarea: Outer Bay (O), Inner Bay (I). Abundance scale in number  $m^{-3}$ : <5 (1), 6–50 (2), 51–200 (3), 201–500 (4), >500 (5).

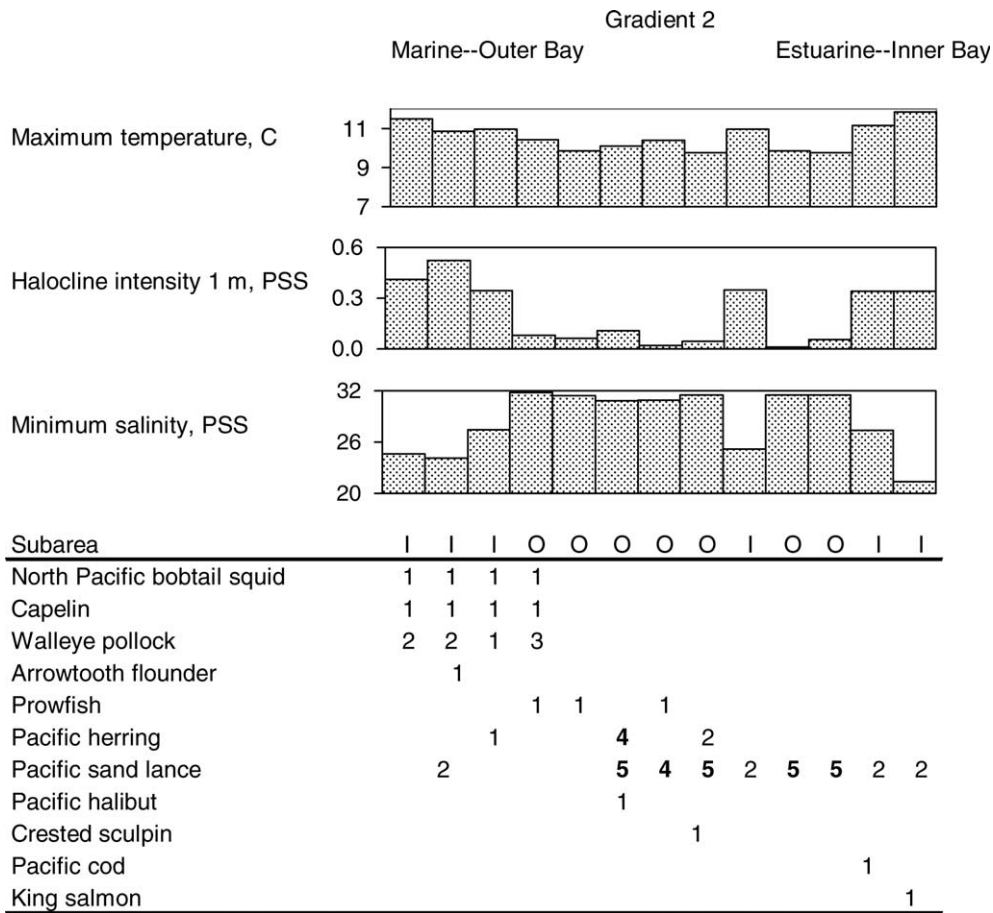


Fig. 12. Detrended correspondence analysis (DCA) ordination of both forage fish species and sampling sites along Gradient 2 in 1999, shown here as the relative position of species and sites along the first DCA axis (eigenvalue = 0.86). See Fig. 8 for explanation. Sites are identified by subarea: Outer Bay (O), Inner Bay (I). Abundance scale in number  $m^{-3}$ : <5 (1), 6–50 (2), 51–500 (3), 501–2000 (4), >2000 (5).

### 3.3. Chlorophyll $\alpha$ : spatial and interannual variability

The gradients in the physical environment poorly explained the abundance and distribution of chlorophyll  $\alpha$ ; most correlations between chlorophyll  $\alpha$  and the PCA of the physical environment were weak (Table 4). Average chlorophyll  $\alpha$  levels for the study area were significantly different among subareas but not between years (2-factor ANOVA after significant MANOVA;  $F_{4,79} = 7.28$ ,  $p < 0.001$  for subarea;  $F_{1,79} = 2.87$ ,  $p > 0.05$  for year). The interaction between subarea and year, however, was significant (ANOVA;  $F_{4,79} = 4.30$ ,  $p < 0.01$ ; Fig. 16(a)). In subareas most influenced by upwelled oceanic waters (Barens, Chugach), average chlorophyll levels were higher in 1999 than in 1998, whereas in the more estuarine subareas, chlorophyll levels were higher in 1998 (Inner Bay) or similar in both years (Chisik, Outer Bay; Fig. 16(a)). Inner Bay especially had high chlorophyll  $\alpha$  levels in 1998, when temperatures were higher (Fig. 15(a) and (b)) and stratification was more pronounced. Average and maximum turbidity levels were significantly lower in 1998 compared to 1999 (Fig. 15(d)), and both subareas with substantial

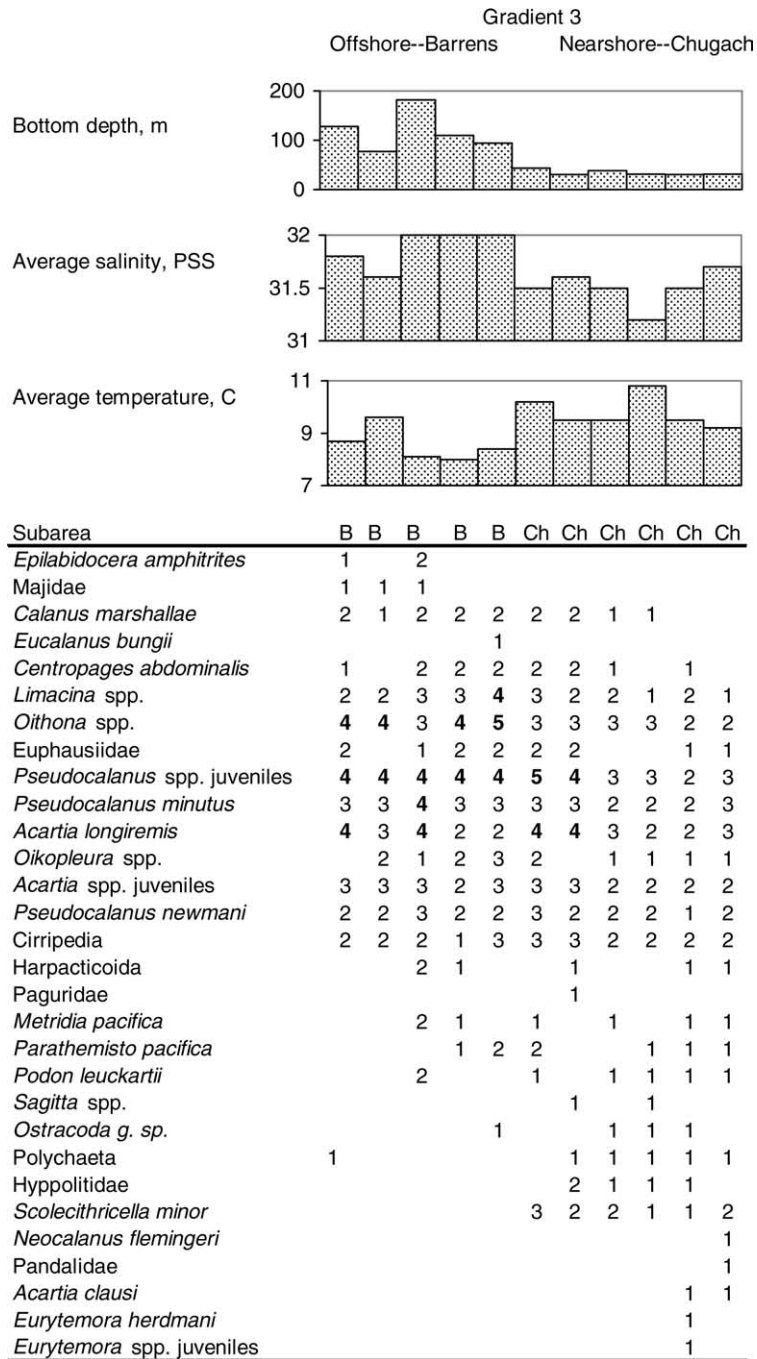


Fig. 13. Detrended correspondence analysis (DCA) ordination of both zooplankton species and sampling sites along Gradient 3 in 1999, shown here as the relative position of species and sites along the first DCA axis (eigenvalue = 0.15). See Fig. 8 for explanation. Sites are identified by subarea: Chugach (Ch), Barrens (B). Abundance scale in number  $m^{-3}$ : <5 (1), 6–50 (2), 51–200 (3), 201–500 (4), >500 (5).

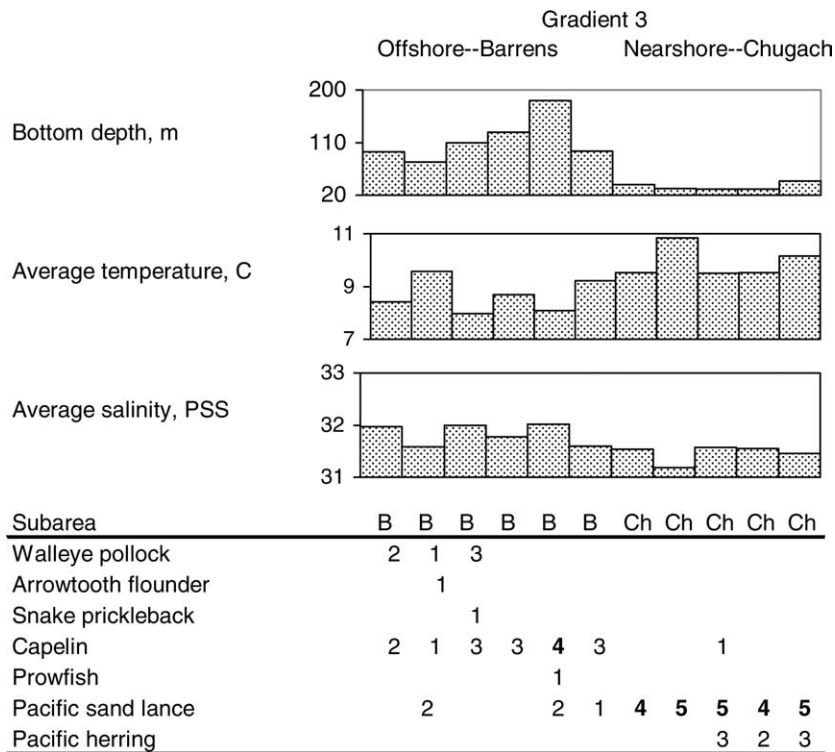


Fig. 14. Detrended correspondence analysis (DCA) ordination of both forage fish species and sampling sites along Gradient 3 in 1999, shown here as the relative position of species and sites along the first DCA axis (eigenvalue = 0.74). See Fig. 8 for explanation. Sites are identified by subarea: Chugach (Ch), Barrens (B). Abundance scale in number  $m^{-3}$ : <5 (1), 6–50 (2), 51–500 (3), 501–2000 (4), >2000 (5).

suspended sediment loads, Chisik and Inner Bay, had lower chlorophyll levels in 1999, when turbidity levels were high. In both years, average chlorophyll  $\alpha$  levels at Chisik were significantly lower than in any other subarea (Scheffé test,  $p < 0.05$ ).

Chlorophyll  $\alpha$  levels at Chisik may have been limited by high average turbidity. An average turbidity threshold existed at about 11 NTU, above which estimated chlorophyll  $\alpha$  levels were depressed to levels below  $4 \mu g l^{-1}$  (Fig. 17(a) and (b)). Such high average turbidity levels occurred exclusively in the Chisik subarea (Figs. 17(c) and 15(d)). Below turbidity levels of 11 NTU, chlorophyll  $\alpha$  levels were variable, ranging from about 2–12  $\mu g l^{-1}$ .

### 3.4. Structure of the zooplankton community: spatial and interannual variability

In all years, the zooplankton community in lower Cook Inlet was numerically dominated by copepods, a mixture of oceanic, neritic, and nearshore species (Appendix I). The most abundant group was juvenile *Pseudocalanus* spp., which were collected at every site and comprised 31% of the total abundance. Other abundant groups were *A. longiremis* (120 sites, 18% of numbers collected), *P. minutus* (113 sites, 11%), *Acartia* spp. juveniles (118 sites, 9%), and *Oithona* spp. (109 sites, 9%). These five groups accounted for 77% of the estimated zooplankton abundance. *Acartia longiremis* occurred at the highest density (4513 individuals  $m^{-3}$ ) in a single tow in the nearshore waters of Inner Bay during 1999. Species richness was highest in the transitional subareas Outer Bay (34 spp.) and Chugach (33 spp.; Fig. 18). The fewest species, 28, were found in

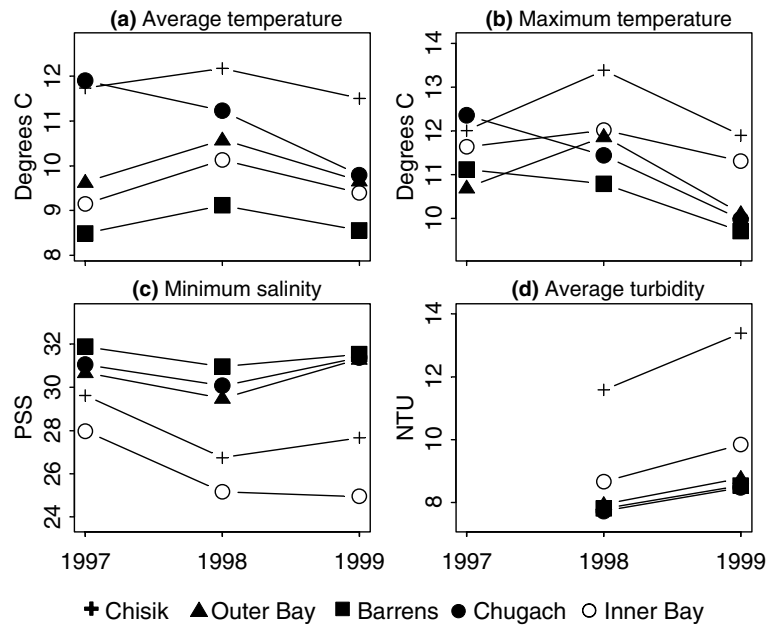


Fig. 15. Interannual variability among the 5 subareas for physical variables that showed significant interannual differences (see Tables 3 and 4).

Table 4

Spearman correlation coefficients of PCA axes 1 and 2 with measures of chlorophyll  $\alpha$  for each year and gradient

		1998		1999	
		PCA axis 1	PCA axis 2	PCA axis 1	PCA axis 2
Gradient 1	Average	0.00	0.20	0.66	0.20
	Maximum	0.21	0.01	0.63	0.48
	Average, top 10 m	0.31	0.00	<b>0.70</b>	0.45
Gradient 2	Average	−0.23	−0.08	−0.10	−0.11
	Maximum	−0.44	0.11	−0.58	−0.56
	Average, top 10 m	−0.14	0.14	−0.52	−0.48
Gradient 3	Average	0.48	0.27	<b>0.73</b>	−0.26
	Maximum	−0.38	−0.63	−0.37	−0.23
	Average, top 10 m	−0.15	−0.54	−0.53	−0.30

The PCA axes summarize the physical environment along each gradient. Correlation coefficients greater than  $\pm 0.70$  are in bold.

Inner Bay and at the Barrens. Slightly fewer zooplankton species were collected within the entire study area in 1998 than in other years (Fig. 18).

Zooplankton density varied significantly by subarea but not by year (2-factor ANOVA;  $F_{4,121} = 18.14$ ,  $p < 0.001$ ;  $F_{2,121} = 0.69$ ,  $p = 0.50$ , respectively; Fig. 16(b)). Densities at the Barrens and in Inner Bay were significantly higher (Scheffé test,  $p < 0.01$ ) than in the other three subareas, whereas densities at Chisik and Chugach were significantly lower (Scheffé test,  $p < 0.01$ ). The interaction between subarea and year was also significant ( $F_{8,121} = 7.68$ ,  $p < 0.001$ ). Spearman's coefficients of rank correlation for zooplankton abundance by species for the 3 years were high:  $r = 0.89$  for 1997 and 1998;  $r = 0.91$  for 1997 and 1999; and  $r = 0.92$  for

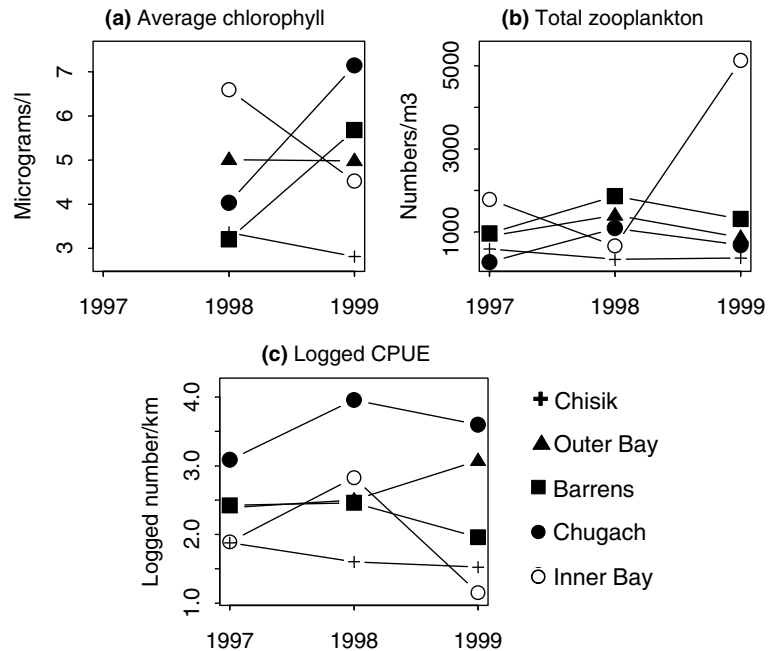


Fig. 16. Interannual variability in the 5 subareas for chlorophyll  $\alpha$  (a), total densities of zooplankton (b), and forage fish CPUE (c).

1998 and 1999. Thus, despite significant changes in abundance of individual taxa among years (see below), dominance among species did not change significantly from 1997 to 1999.

We selected six common and ecologically important taxa for detailed analysis: *A. clausi*, *A. longiremis*, *P. minutus*, *Oikopleura* spp., *Oithona* spp., and *Limacina* spp. (Fig. 19). Three of the six species (*A. longiremis*, *P. minutus*, and *Oikopleura* spp.) showed significant interannual differences (MANOVA;  $V_{12,204} = 0.72$ ,  $p < 0.001$  for year), whereas all six species showed significant spatial differences ( $V_{24,416} = 1.38$ ,  $p < 0.001$  for subarea; see Speckman, 2004). The patterns of interannual differences were varied, but the spatial patterns were consistent with known differences in oceanography. The most marine species (*Limacina* spp., *Oithona* spp.; Fig. 19(a) and (b)) peaked in abundance at the Barrens. Neritic species (*P. minutus*, *Oikopleura* spp.; Fig. 19(c) and (d)) were abundant in all subareas except Chisik, the most estuarine. The species with the highest abundance in the Chisik subarea were *A. longiremis* and *A. clausi* (Fig. 19(e) and (f)). *Acartia* spp. abundance, however, was highest in Outer and Inner bays. A unique and marked pattern of abundance was exhibited by seven of the eleven most abundant taxa (Appendix I) in the study area: *A. clausi*, *A. longiremis*, *Acartia* juveniles, *P. minutus*, *P. newmani*, *Pseudocalanus* juveniles, and *Scolecithricella minor*. All showed a sharp decline in numbers in 1998 compared to 1997, and an even sharper recovery in 1999 (Fig. 19(c), (e) and (f)).

### 3.5. Structure of the forage fish community: spatial and interannual variability

Analyses of mid-water trawls were limited to tows that captured at least 5 fish of any one species or a total of 10 fish, yielding a total of 101 trawls during the 3-year study: 34 in 1997, 32 in 1998, and 35 in 1999. Only fishes  $< 200$  mm in length were included in analyses; larval fish were excluded. In all years, the fish community in lower Cook Inlet was numerically dominated by Pacific sand lance, which comprised 70% of captured fish (Appendix II). Sand lance were caught at 76 trawl sites. Other abundant species were Pacific

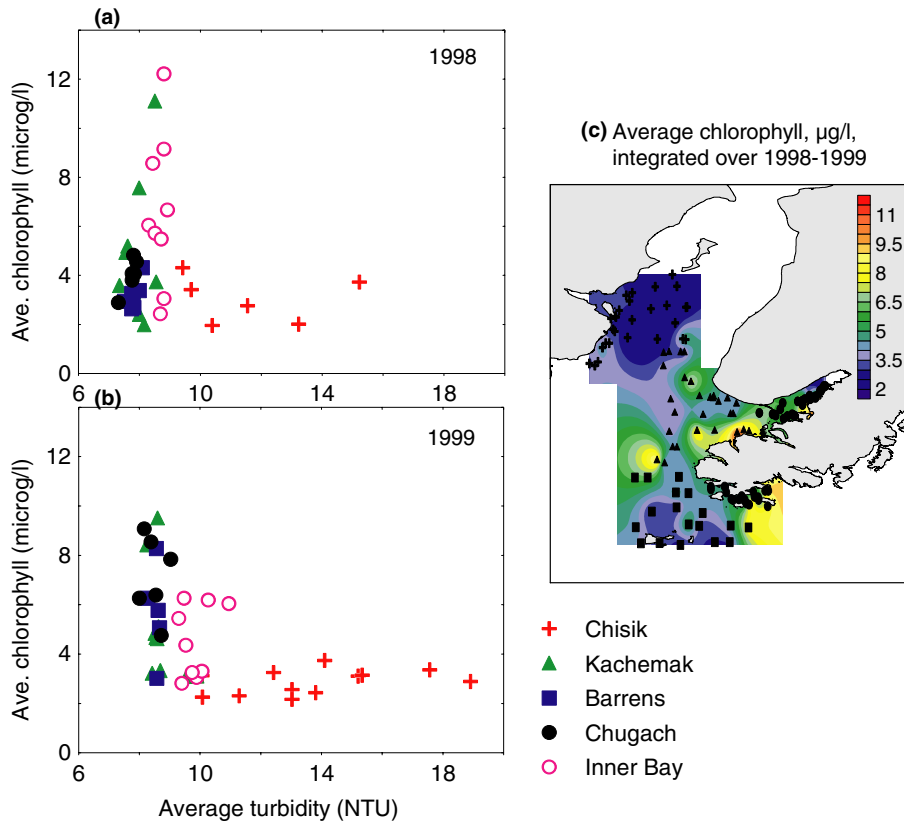


Fig. 17. (a, b) High turbidity appears to limit primary production (approximated by chlorophyll  $\alpha$  standing stocks), especially in the Chisik subarea. (c) Spatial variability in chlorophyll  $\alpha$  levels.

herring (51 sites, 17% of captured fish), walleye pollock (43 sites, 10% of captured fish), and capelin (30 sites, 2% of captured fish). These four groups accounted for almost 99% of the total catch in numbers. Species richness was highest in the most estuarine subarea, Chisik, and decreased to the south as waters became more marine (Fig. 18). Only four species (sand lance, herring, capelin, and Pacific cod) were captured at Chugach. Species richness for the entire study area dropped by 50% from 1997 (30 spp.) to 1998 (15 spp.; Fig. 18). By 1999, species richness had recovered.

Total forage fish CPUE varied significantly by subarea but not by year (2-factor ANOVA;  $F_{4,101} = 17.85$ ,  $p < 0.001$ ;  $F_{2,101} = 0.73$ ,  $p = 0.48$ , respectively; Fig. 16(c)). CPUE at Chugach was significantly higher (Scheffé test,  $p < 0.001$ ) than in the other four subareas. CPUE at Chisik was significantly lower than in Outer Bay (Scheffé test,  $p < 0.01$ ). The interaction between subarea and year was also significant ( $F_{8,101} = 2.33$ ,  $p < 0.05$ ; Fig. 16(c)). Spearman's coefficients of rank correlation for forage fish abundance by species for the 3 years were much lower than for zooplankton:  $r = 0.44$  for 1997 and 1998;  $r = 0.60$  for 1997 and 1999; and  $r = 0.48$  for 1998 and 1999. Although interannual differences in total CPUE were not significant, CPUE of several common forage fish varied significantly among years (MANOVA;  $V_{12,164} = 0.31$ ,  $p < 0.01$ ; see Speckman, 2004), including herring, capelin, and pollock. Pollock catches were significantly higher in 1997 than in 1999 (Scheffé test,  $p < 0.001$ ); herring catches were highest in 1998 (Scheffé test,  $p < 0.05$  for 1997 and  $p < 0.01$  for 1999); and capelin catches were highest in 1999 (Scheffé test,  $p < 0.05$  for both years; Fig. 20(a), (b), and (d)).

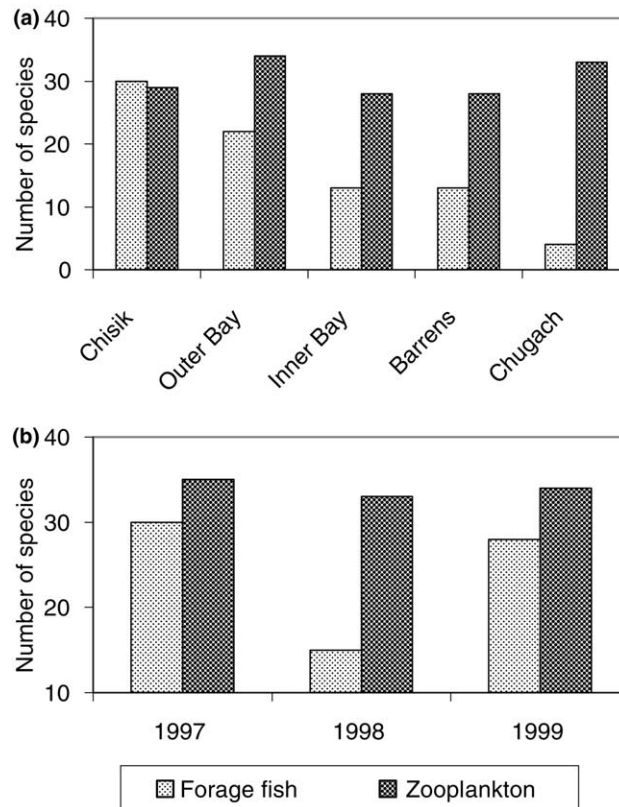


Fig. 18. Zooplankton and forage fish species richness by subarea (a) and by year (b).

Catches of the six forage fish species varied significantly among subareas (MANOVA;  $V_{24,336} = 1.28$ ,  $p < 0.001$ ; Fig. 20). Longfin smelt and Pacific sandfish dominated the turbid, warm, low-salinity Chisik subarea, although CPUE was low for each (Fig. 20(c) and (e)). Longfin smelt were not found outside the Chisik subarea, and sandfish were found in low numbers in Outer Bay. Capelin were most common in the deep, cold, marine waters of the Barrens, and a pulse of capelin showed up at Chisik in 1999 (Fig. 20(b)). Walleye pollock were also most common in the deep waters of the Barrens, and were caught in high numbers in Outer Bay in 1997 (Fig. 20(d)). Sand lance were most abundant in the shallow, coastal waters at Chugach (Fig. 20(f)), although they were captured in all subareas in all years. Finally, herring were caught in all subareas except the Barrens, where they were absent in all three years of the study. Herring catches were highest at Chugach in all years, especially in 1998 (Scheffé test,  $p < 0.001$ ; Fig. 20(a)). Overall, three of the six species examined in detail showed significant interannual differences, and all six showed significant spatial differences.

### 3.6. Relating biological structure to the physical environment

Although defining subareas is a useful tool that allows us to detect statistically significant spatial and temporal differences in biology and physics, the spatial patterns that we found across the lower estuary are continuous. Abundance of zooplankton taxa shifted along all three of the physical oceanographic gradients identified by the PCA. Correlations between the zooplankton DCA axes and corresponding physical PCA

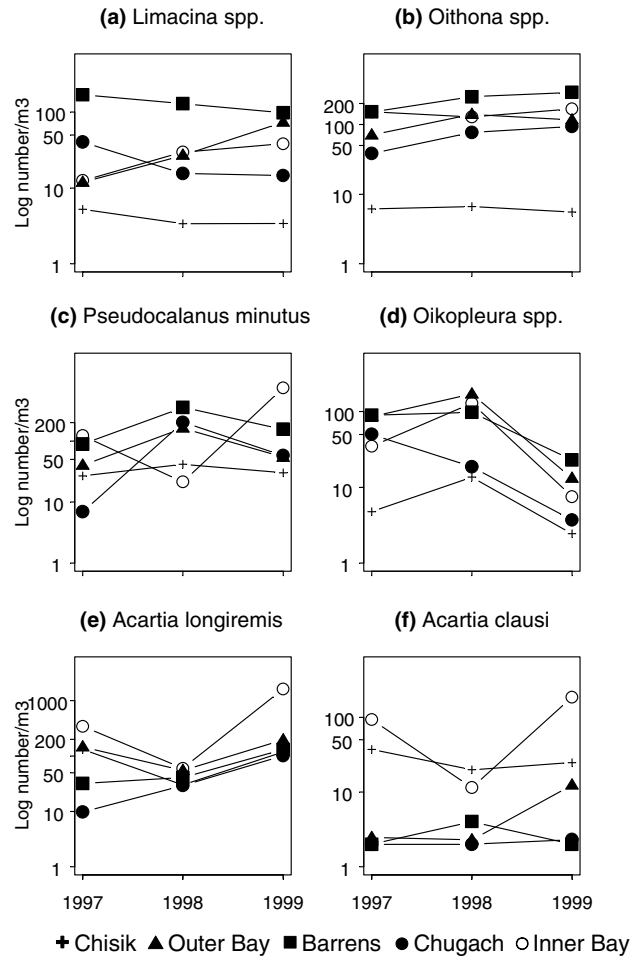


Fig. 19. Average densities of 6 taxa of zooplankton  $\text{m}^{-3}$  by subareas and years.

axes for Gradients 1 and 2 were high (Table 5), indicating that within each year, the zooplankton community structure captured by the DCA paralleled the structure of the physical environment as identified by the first principal component (which itself accounted for 35–45% of total variance in the physical signal; Table 3). Zooplankton DCA axis 3 and PCA axes along Gradient 3 were poorly correlated, indicating that zooplankton species composition was similar between the Barrens and Chugach. Structure of the forage fish community was highly correlated with structure of the physical environment along Gradient 1 in 1997 and 1998, and along Gradient 3 in all years. Correlations between the forage fish DCA axes and corresponding physical PCA axes along Gradient 2 were low in all years (Table 5), indicating that species composition of midwater forage fish catches in Inner and Outer Kachemak Bay did not differ significantly. In 1999, forage fish communities along Gradients 1 and 2 underwent a marked change, evidenced by the low correlation between the DCA axis and corresponding physical PCA axes. This change may have been due to factors we did not measure, because fish distribution and abundance along Gradient 1 in 1999 were poorly explained by turbidity, temperature and salinity structure. Pollock, capelin, and arrowtooth flounder were present at

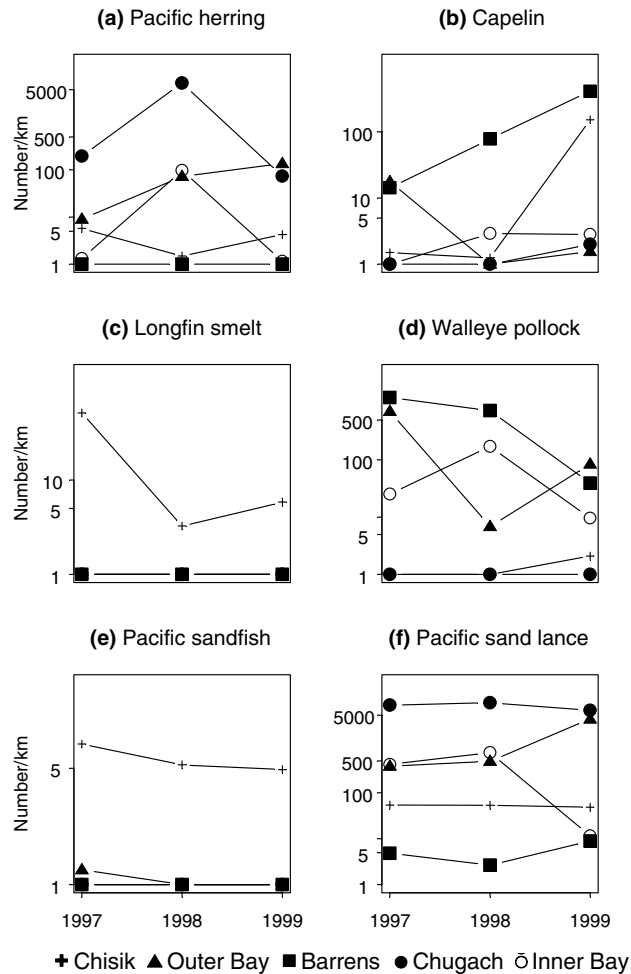


Fig. 20. Average catch-per-unit-effort (CPUE) of 6 taxa of forage fish by subareas and years.

Chisik but not at Outer Bay, making Chisik more similar to the Barrens subarea, and supporting the idea that Outer Bay was unusual in 1999.

Mantel tests substantiate the parallel structuring between fish and zooplankton biology and physics (Table 6). A significant correlation between the physical matrix and the zooplankton community structure matrix (DCA scores) indicates that zooplankton species composition (community structure) shifted along physical gradients. Likewise, a significant correlation between the physical matrix and the forage fish community structure matrix (DCA scores) indicates that forage fish community structure shifted along the same physical gradients. Chlorophyll  $\alpha$  levels for 1998 and 1999 were weakly correlated with the physical environment and zooplankton community structure. The model matrix for the 5 subareas was significantly correlated with all abiotic and biotic matrices (Table 6), confirming results from the multivariate analyses that spatial differences exist in the structure of the physical environment; chlorophyll  $\alpha$  levels; zooplankton community and density; and forage fish community. Interannual differences in structure were significant for the physical environment, zooplankton community, and forage fish community, indicating that interannual changes in the physical environment may have structuring effects on successive trophic levels. Chlorophyll

Table 5

Spearman correlation coefficients (*r*) of PCA axes 1 and 2 with DCA axis 1 for each year and gradient

		1997		1998		1999	
		PCA axis 1	PCA axis 2	PCA axis 1	PCA axis 2	PCA axis 1	PCA axis 2
Zooplankton							
DCA axis 1	Gradient 1	<b>0.74</b>	0.40	<b>0.86</b>	0.04	<b>0.85</b>	0.33
	Gradient 2	<b>0.79</b>	0.25	<b>0.84</b>	0.12	<b>0.81</b>	0.15
	Gradient 3	0.50	0.13	0.43	0.35	0.56	0.05
Forage fish							
DCA axis 1	Gradient 1	<b>0.87</b>	0.40	<b>0.82</b>	0.28	0.32	0.50
	Gradient 2	0.46	<b>0.79</b>	0.27	0.39	0.22	0.45
	Gradient 3	<b>0.78</b>	0.10	<b>0.77</b>	<b>0.70</b>	<b>0.75</b>	0.15

The PCA axes summarize the physical environment along each gradient, and the DCA axes summarize zooplankton or forage fish community structure.

$\alpha$  levels and zooplankton total density and biomass did not vary significantly among years. All abiotic and biotic matrices (except forage fish) were positively correlated with geographic distance, indicating that closer sites were more similar than distant sites.

## 4. Discussion

### 4.1. Parallel structuring

Our examination of physical-biological linkages in lower Cook Inlet is consistent with the concept of “bottom-up control,” i.e., that variability in the physical environment structures higher trophic communities by influencing their distribution and abundance across time and space. The abundance and distribution of phytoplankton, zooplankton and forage fish were affected much more by spatial variability in physical oceanography than by interannual variability. We found that the spatial variability in the physical oceanographic environment in lower Cook Inlet can be modeled as three marine-estuarine gradients. The gradients persisted throughout the three years of this study and could be defined by measures of temperature, salinity, bottom depth, and turbidity, which captured both horizontal and vertical heterogeneity in the water column.

Both Mantel tests and correlations between PCA and DCA axes showed that, overall, spatial patterns of variability in biological communities paralleled patterns of variability in the physical environment. The links between chlorophyll  $\alpha$  levels and the physical oceanography, zooplankton, and forage fish were weak (Table 6). Using estimated chlorophyll  $\alpha$  standing stocks instead of rates of primary production may have limited our ability to demonstrate stronger correlations with the physical environment and higher trophic levels. Chlorophyll  $\alpha$  standing stocks can be heavily influenced by zooplankton grazers, variations in species composition, physiological condition of the phytoplankton, and other factors (Falkowski & Raven, 1997; Strom, Brainard, Holmes, & Olsen, 2001; Valiela, 1995). Additionally, the spatial scale at which we sampled (point locations) may not have been appropriate for detecting coherence between chlorophyll and zooplankton, which can be patchy at varying scales (Mackas, Denman, & Abbott, 1985). Significant correlations have been detected between concentrations of chlorophyll and zooplankton at scales of 1 km and larger (Mackas, 1984; Mackas & Boyd, 1979; Star & Mullin, 1981). When considered at the scale of the five subareas, levels of chlorophyll  $\alpha$  in lower

Table 6  
Summary of Mantel test statistics,  $r$

		Physical environment		Phytoplankton chlorophyll $\alpha$		Zooplankton species ordination (DCA)		Zooplankton density and biomass		Fish species ordination (DCA)	
		$r$	$p$ -value	$r$	$p$ -value	$r$	$p$ -value	$r$	$p$ -value	$r$	$p$ -value
All Years	Zooplankton species ordination (DCA)	<b>0.24</b>	<b>0.0001</b>								
	Fish species ordination (DCA)	<b>0.19</b>	<b>0.0001</b>			<b>0.21</b>	<b>0.0001</b>				
	Geographic distance	<b>0.33</b>	<b>0.0001</b>			<b>0.57</b>	<b>0.0001</b>	<b>0.16</b>	<b>0.0001</b>	0.01	0.4070
	Subareas (model)	− <b>0.38</b>	<b>0.0001</b>			− <b>0.33</b>	<b>0.0001</b>	− <b>0.13</b>	<b>0.0001</b>	− <b>0.23</b>	<b>0.0001</b>
	Years (model)	− <b>0.04</b>	<b>0.0016</b>			− <b>0.06</b>	<b>0.0003</b>	−0.01	0.0957	− <b>0.07</b>	<b>0.0001</b>
1998–1999	Phytoplankton chlorophyll $\alpha$	0.09	0.0479								
	Zooplankton species ordination (DCA)			0.09	0.0402						
	Fish species ordination (DCA)			0.05	0.2092						
	Geographic distance			<b>0.18</b>	<b>0.0001</b>						
	Subareas (model)			− <b>0.14</b>	<b>0.0001</b>						
	Years (model)			0.00	0.3663						

Mantel tests estimate the association between two independent dissimilarity matrices that describe the same set of samples. Significance was set at  $p = 0.0024$  after applying the Bonferroni correction for multiple tests ( $N = 21$ ). Significant tests are shown in bold.

Cook Inlet were highly correlated with abundance of zooplankton and forage fish and physical oceanography.

The differences in physical oceanography among subareas were statistically significant, but more importantly, they were biologically significant in that each subarea supported a unique community of zooplankton and forage fish species. Differences in the abundance and availability of prey would affect higher trophic-level predators such as seabirds and marine mammals by presenting them with different energetic returns (Robards et al., 2002). This may be especially important for seabirds during the breeding season, when their foraging range is restricted to areas near their colonies and rearing of chicks requires high-energy foods (Anker-Nilssen, Barrett, & Krasnov, 1997). The three seabird colonies located within our study area are surrounded by markedly different oceanographic regimes (this study; Abookire & Piatt, 2005; Robards, Piatt, Kettle, & Abookire, 1999; Robards et al., 2002). Seabirds at the Chisik colony (high turbidity and low productivity) encounter low abundances of longfin smelt, salmon, and sandfish, all of which have low energy content (Anthony, Roby, & Turco, 2000). Some birds nesting at Chisik usually suffer low reproductive success or complete breeding failure (Piatt, 2002). Seabirds at the Barrens, within foraging range of the highly productive Chugach subarea and high numbers of energy-dense (Van Pelt, Piatt, Lance, & Roby, 1997) sand lance and herring, do well in nearly all years (Piatt, 2002). Thus, the effects of “bottom-up” forcing appear to propagate through the food web, influencing the distribution and abundance of higher trophic level animals including zooplankton, forage fish, and seabirds.

#### 4.2. Major structuring factors: turbidity

Turbidity was a dominant structuring force in this estuarine system. Large quantities of glacially-derived sediments enter upper Cook Inlet from rivers, and strong currents in the upper part of the inlet and around the Forelands prevent the sediments from being deposited. Most of the silt and clay is transported through the Forelands (Fig. 1), southward along the western side of lower Cook Inlet (Sharma & Burrell, 1970), and through the Chisik subarea where suspended sediment concentrations peak in early spring, around April (Feely & Massoth, 1982). Several smaller rivers contribute suspended sediment directly into the lower inlet, including Inner Kachemak Bay (Feely & Massoth, 1982).

Effects of turbidity appeared to be strongest on chlorophyll  $\alpha$  levels, which were greatly reduced in highly turbid areas. The trend we found, of diminishing chlorophyll  $\alpha$  levels in the direction of high turbidity, is common in estuaries (Goosen, Kromkamp, Peene, van Rijswijk, & van Breugel, 1999; Mallin, Cahoon, McIver, Parsons, & Shank, 1999; Stockner, Cliff, & Buchanan, 1977). Turbidity reduces primary production by increasing light attenuation. Larrance et al. (1977) found that the area near Chisik Island had very low primary productivity throughout summer, and determined that maximum production was about one-tenth of that in Kachemak Bay. Additional processes that can cause low chlorophyll  $\alpha$  levels in estuarine habitats include flushing from the estuary (Stockner et al., 1977) and mixing below the critical depth (Irigoin & Castel, 1997). It is not known what role these factors played in lower Cook Inlet. Average turbidity levels in Outer Bay, the Barrens, Chugach, and Inner Bay were always below 11 NTU, the level above which chlorophyll  $\alpha$  levels were dramatically reduced. In Inner Bay, sediments were suspended in a layer near the surface, not mixed throughout the water column. Chlorophyll  $\alpha$  levels in Inner Bay were variable, likely due to patchiness of the layers carrying suspended sediment, and could be very high when conditions were favorable. High sediment loads at Chisik were associated with low chlorophyll  $\alpha$  levels.

Low chlorophyll  $\alpha$  levels at Chisik do not appear to result from lack of nutrients. Nutrient data are limited, but sampling along an east-west transect across the lower inlet indicated that in midsummer 1997 total nitrogen and silica levels on the western side of lower Cook Inlet were high, about 6 and 14  $\mu\text{M}$ , respectively (Piatt, 2002). At the same locations, chlorophyll  $\alpha$  levels were very low,  $<2.0 \mu\text{g l}^{-1}$ . Toward the

east along the same transect, chlorophyll  $\alpha$  levels increased at least 6-fold as nitrogen and silica levels declined by about two-thirds. At the eastern-most station, both nutrient and chlorophyll  $\alpha$  levels were low, indicating possible nutrient depletion at that station. Larrance et al. (1977) determined that during spring and summer, nutrients can be limiting in the upper mixed layer of productive areas in lower Cook Inlet. Factors that we did not measure probably explain much of the variability in chlorophyll  $\alpha$  where turbidity was not the limiting factor. Correlations between estimated chlorophyll  $\alpha$  and the physical environment for both the PCA axes and the Mantel tests were weak (Tables 4 and 6). Our analyses of temperature, salinity, bottom depth, and turbidity marginally explained the abundance and distribution of chlorophyll  $\alpha$  at this large spatial scale.

Several zooplankton species, including *Eurytemora herdmanni*, *Tortanus discaudatus*, and *A. clausi*, had peak abundance in highly turbid subareas, but their overall densities were very low: <200 individuals  $\text{m}^{-3}$  for *A. clausi* in Inner Bay, <50 individuals  $\text{m}^{-3}$  at Chisik, and <30 individuals  $\text{m}^{-3}$  for the other species. Low chlorophyll  $\alpha$  levels resulted in a decreased capacity for production at higher trophic levels. Highly turbid systems can negatively affect zooplankton because the indigestible suspended particles dilute their food (Herman & Heip, 1999). Estuarine copepods are selective feeders (Gasparini & Castel, 1997; Tackx, Zhu, De Coster, Billones, & Daro, 1995). *Eurytemora affinis*, for example, is able to feed selectively to some extent on phytoplankton cells, even when suspended particulate matter concentrations are high, but egg production decreases strongly as suspended particulate matter inhibits the uptake of microplankton (Burdloff, Gasparini, Sautour, Etcheber, & Castel, 2000). Both growth rate and egg production in *A. clausi* decrease as food becomes scarce (Sekiguchi, McLaren, & Corkett, 1980). These factors may contribute to the low zooplankton densities observed at Chisik.

Longfin smelt, juvenile salmon, sandfish, and lamprey were found exclusively or nearly so in the turbid, warm, low-salinity waters near Chisik, and sand lance were found regularly in this area. Of these, all but lamprey can feed on zooplankton. Feeding by piscivores is substantially more sensitive to elevated turbidity than feeding by planktivores (De Robertis, Ryer, Veloza, & Brodeur, 2003). De Robertis et al. (2003) found that at a turbidity level of 10 NTU, a piscivorous predator was unable to capture its prey, whereas feeding by two planktivores was unaffected. Elevated turbidity may be advantageous for planktivorous fish because they are less vulnerable to predatory fishes (De Robertis et al., 2003; Gregory & Levings, 1998) without having to give up feeding opportunities. In our study, high average turbidity levels near Chisik (9–19 NTU) may make this area a refugium for longfin smelt, sandfish, and juvenile salmon by reducing predation. Availability of turbid estuarine habitats that provide protection from predators may be especially important for young salmon, which utilize estuaries as they adapt to marine conditions (Linley, 2001; Simenstad, Fresh, & Salo, 1982). Lamprey and sandfish are more active at night than during the day (Mecklenburg, Baxter, Mecklenburg, & Thorsteinson, 2002; Moser, Matter, Stuehrenberg, & Bjornn, 2002) and, therefore, may be adapted to low-light conditions. Lamprey have well-developed olfactory and lateral line systems and possess several types of chemoreceptive cells (Braun, 1996) that they may use to locate prey. Sandfish are poorly known, but may also have special adaptations (e.g., ability to track hydrodynamic or chemical tracks) that enable them to forage efficiently under conditions of low visibility.

There may be costs, however, associated with highly-turbid habitats with low productivity. Robards et al. (2002) found that sand lance at Chisik grew slower and were smaller at age than sand lance in more productive habitats in lower Cook Inlet. Additionally, muddy substrates in turbid areas such as Chisik are unsuitable for burrowing by sand lance (Robards et al., 2002).

#### 4.3. Major structuring factors: temperature and salinity

Temperature and salinity, which exhibited similar spatial patterns, were important components of every marine-estuarine gradient we defined in lower Cook Inlet. Strong correlations between measures of temperature and salinity, however, limited our ability to separate their effects on communities. Differences in

phytoplankton distributional trends across an estuary often reflect their tolerances to salinity, because salinity directly influences rates of phytoplankton cell division as well as distribution of phytoplankton species (Flameling & Kromkamp, 1994; Kennish, 1990). Differences in species composition may have influenced our measurements of chlorophyll  $\alpha$  levels. Temperature alone likely did not have important direct effects on chlorophyll  $\alpha$  standing stocks (Falkowski & Raven, 1997; Valiela, 1995) within the range of temperatures measured in our study area. For example, Star and Mullin (1981) found no correlation between temperature and chlorophyll in the North Pacific, a large spatial scale. The highest chlorophyll  $\alpha$  levels that we measured occurred in Inner Bay, which is characterized by strong stratification at thermoclines and haloclines. Development of a strong thermocline as seen in Inner Bay can have significant indirect effects on phytoplankton by fostering greater stability of the water column and enhancing production (Kennish, 1990).

We found that responses of zooplankton to temperature and salinity gradients varied among species, as has been found in other areas (Mackas, Thomson, & Galbraith, 2001; Samatov & Samatova, 1996; Vinas, Negri, Ramirez, & Hernandez, 2002). Abundance patterns of zooplankton among subareas varied relatively little among years, with the notable exception of Inner Bay. Some of the variation we observed in zooplankton numbers among subareas and years likely resulted from differences in the timing of reproduction. Although cruises were limited to a 3-week period each summer, differences in the timing of our cruises from year to year may also have affected our measurements of zooplankton densities.

Similarly, responses of forage fish to temperature and salinity gradients also varied among species, as documented in other areas (Castillo et al., 1996; Paramo, Quiñones, Ramirez, & Wiff, 2003). We found that, within the range of temperatures and salinities we sampled, forage fish were distributed along gradients of temperature and salinity (as well as additional factors). For example, longfin smelt and Pacific sandfish utilized habitats characterized by low salinity and warm temperatures, whereas capelin and walleye pollock were found in cold, more saline waters. Effects of variability in temperature, salinity, and fishing depth on the midwater fish community in lower Cook Inlet have also been examined by Abookire and Piatt (2005). In agreement with our results, they found that the overall forage fish community in lower Cook Inlet was structured by temperature and salinity, the effects of which were difficult to separate. They determined that different oceanographic conditions structured forage fish into communities that are lipid-rich (Barrens, Kachemak; colder, deeper, more saline water) and lipid-poor (Chisik; warmer, shallower, less saline water).

Effects of temperature and salinity on forage fish distribution and abundance in lower Cook Inlet have been separated somewhat by Speckman (2004). She found that the density of single-species forage fish schools, measured using hydroacoustics and converted to fish  $\text{m}^{-3}$ , varied with average temperature, maximum salinity, fishing depth, bottom depth, and average turbidity. The highest densities of sand lance, herring, longfin smelt, and sandfish were captured primarily near the surface (<40 m) in shallow (40 m), warm (9–12 °C) waters. Longfin smelt and sandfish densities were higher in fresher (29–30 PSS), more turbid (11–19 NTU) waters, whereas sand lance and herring densities peaked in more saline (30 PSS), clearer waters (7 NTU). In contrast, capelin and especially walleye pollock were captured much deeper (50–110 m) in deep-water areas (70–170 m) typified by cold (7–8 °C), saline (31–32 PSS), clear (7–9 NTU) waters. Studies of forage fish in other areas corroborate our results. In Prince William Sound, age-0 pollock schools were found primarily in deep waters, below the depths of herring and sand lance schools (Thedinga, Hulbert, & Coyle, 2000). Juvenile herring in Prince William Sound aggregated in shallow, nearshore areas (Stokesbury, Kirsch, Brown, Thomas, & Norcross, 2000). Sand lance, nearly ubiquitous in lower Cook Inlet, have been shown to utilize a wide range of estuarine and shelf habitats (this study; Abookire & Piatt, 2005; McGurk & Warburton, 1992; Robards et al., 2002).

We found significant differences between Inner Bay and Outer Bay in physical oceanography (Inner Bay had warmer maximum temperatures, was more strongly stratified, and had lower salinity minima). We also found significant differences in the densities of the two most abundant zooplankton species, *A. clausi* and

*A. longiremis*. Zooplankton community structure was highly correlated with the physical gradient along Gradient 2, which runs through the two sites. Differing zooplankton distributions along Gradient 2 may result from the different vertical salinity gradients (haloclines) that characterize these two subareas, and are known to elicit unique responses from zooplankton species (Lougee, Bollens, & Avent, 2002).

We found no significant differences between Inner and Outer bays in total forage fish CPUE or in the CPUE of the six fish species we examined individually, and forage fish community structure was not correlated with the physical gradient along Gradient 2. This may indicate that the linkages between the physical and biological environments, at least in this area, were weaker at higher trophic levels. In contrast to our results, Abookire et al. (2000) found significant differences between forage fish communities in Inner and Outer bays that were sampled with seines. Their findings may reflect differences in distribution due to beach substrates, which have less influence on the distribution of fish in the water column.

#### 4.4. Interannual variability in climate

Occurrence of the 1997–1998 El Niño event was documented throughout the North Pacific (PICES Scientific Report, 1999) and in Cook Inlet (Piatt et al., 1999). El Niño signals propagated through the atmosphere were first detected in the Gulf of Alaska in about June of 1997 as increased sea surface temperatures (Overland, Bond, & Adams, 2001). Later, in the winter of 1997–1998, deep-water (250 m) effects were measured, as a pulse of anomalously warm water was tracked up the western coast of North America and along the coast of Alaska as part of the Alaska Coastal Current (Freeland & Whitney, 2000; Royer & Weingartner, 1999). This deep-water signal was lost in the eastern Gulf of Alaska in the spring of 1998, when temperatures there returned to normal, remaining so for the summer of 1998 (Whitney & Welch, 2002). During the El Niño event in the Gulf of Alaska, salinity levels were lower than normal (Freeland & Whitney, 2000).

We detected elevated surface temperatures in the two outermost subareas (the Barrens and Chugach) in 1997, but not increased average water temperatures, which is consistent with the idea of atmospheric coupling between the northern Gulf of Alaska and lower latitudes (Overland et al., 2001). We measured higher average and surface temperatures and lower salinities throughout our study area in lower Cook Inlet in the summer of 1998 (this study; Piatt, 2002). It is not clear whether residual effects of the El Niño event accounted for the increased temperatures observed in lower Cook Inlet during 1998. All of the signals we detected were weak, probably because they were mediated by local oceanographic conditions, but they paralleled the El Niño effects seen in the open Gulf of Alaska. El Niño events, then, may be able to penetrate into the far “corners” of the North Pacific Ocean, and their signals may be detectable in the variable physical conditions found in northern estuaries like Cook Inlet (Piatt, 2002; Piatt et al., 1999).

Interannual variability in temperature and salinity in lower Cook Inlet was not strongly propagated up the food web to zooplankton and forage fish. Average chlorophyll  $\alpha$  levels did not vary significantly from 1998 to 1999. Neither total zooplankton abundance nor total CPUE for forage fish varied significantly among years, whereas both varied significantly among subareas. Similarly, Peterson and Keister (2002) found that copepod biomass off the Oregon and northern California coasts did not differ between 1998 and 1999. Interannual differences in zooplankton community structure were minimal. Interannual differences in forage fish community structure were greater, with weaker correlations among years and a substantial restructuring that occurred along Gradient 1 in 1999. Overall, however, spatial variability among physical oceanographic variables was a much greater structuring factor than interannual variability, and affected higher trophic levels that were organized along the physical estuarine gradients.

#### 4.5. Evidence for top-down structuring

We also found evidence that top-down effects may be altering biological structure. The opposite patterns exhibited by chlorophyll  $\alpha$  levels and zooplankton abundance in Inner Bay in 1998 and 1999 may be

evidence of top-down control of phytoplankton, since very high numbers of grazers coincided with low chlorophyll  $\alpha$  levels. Low zooplankton abundance in 1998 may have allowed high chlorophyll levels to accrue. In 1999 in Inner Bay, a population explosion of copepods occurred that likely grazed down chlorophyll levels, reducing them to levels below those of 1998.

A second example of a top-down effect may have occurred at Chugach, where relatively low densities of zooplankton contrasted with extremely high fish catches. High fish catches, however, likely indicate high fish densities overall. The predominant species, sand lance and herring, were young (age-0 and 1; Piatt, 2002) and consume zooplankton, mostly copepods (Blackburn & Anderson, 1997; Willette, Sturdevant, & Jewett, 1997). High fish densities could have reduced zooplankton numbers through predation.

#### 4.6. Conclusions

Lower Cook Inlet is part of a dynamic estuary with significant spatial variability in every physical variable that we measured. Our results showed that this spatial heterogeneity in physical oceanography results in variable productivity among subareas, including significant differences in chlorophyll  $\alpha$  levels, species composition of zooplankton and forage fish, and overall abundance of zooplankton and forage fish (this study; Abookire & Piatt, 2005; Abookire et al., 2000; Robards et al., 2002). Although top-down effects appeared to impact localized parts of our study area, “bottom-up” effects were a stronger, inlet-wide structuring influence.

Although differences among subareas in temperature and salinity in lower Cook Inlet were seemingly small, differences among subareas in abundance and species composition of both zooplankton and forage fish were usually substantial. Persistent and dramatic changes in community structure have been documented for the Gulf of Alaska, including Cook Inlet, which have been linked to climate variability within the past few decades (Anderson & Piatt, 1999; Francis, Hare, Hollowed, & Wooster, 1998; Hare & Mantua, 2000). Future temperature changes on the scale of those predicted by global climate models (see Karl & Trenberth, 2003, for reviews; Stenseth et al., 2002) could result in similarly dramatic changes in distribution and abundance of marine organisms, or even the gain (or loss) of species. Our results advance our understanding of how variability in the physical marine environment influences the distribution and abundance of higher trophic levels, and how changing climate may affect marine systems.

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# Appendix I

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List of zooplankton species and taxa collected from 1997 to 1999 in Lower Cook Inlet, Alaska. Sites: number of sites (121 possible) at which each group was collected; Number: estimated total number of individuals collected; and Rank: rank order of abundance. Groups shown are those used for analyses.

Phylum	Subphylum	Class	Subclass	Order	Suborder	Family	Genus	Species	Sites	Number	Rank
Nemata (Nematoda)		—	—	—		—	—	—	5	163	33
Mollusca		Bivalvia	—	—		—	—	—	28	2549	21
		Gastropoda	—	Thecosomata (Pteropoda)		Limacinidae	<i>Limacina</i>	spp.	98	56,621	8
							<i>Clione</i>	<i>limacina</i>	1	14	39
Annelida		Polychaeta	—	—		—	—	—	63	5447	16
Arthropoda	Crustacea	Ostracoda	—	—		—	—	—	46	1390	23
		Maxillapoda	Copepoda	Calanoida		Acartiidae	<i>Acartia</i>	<i>clausi</i>	50	25,962	11
							<i>Acartia</i>	<i>longiremis</i>	120	295,242	2
							<i>Acartia</i>	spp. juveniles	118	139,808	5
						Paracalanidae	<i>Calanus</i>	<i>marshallae</i>	76	14,338	13
						Centropagidae	<i>Centropages</i>	<i>abdominalis</i>	113	23,264	12
						Pontellidae	<i>Epilabidocera</i>	<i>amphitrites</i>	24	687	29
						Eucalanidae	<i>Eucalanus</i>	<i>bungii</i>	20	903	26
						Temoridae	<i>Eurytemora</i>	<i>herdmani</i>	34	3650	19
							<i>Eurytemora</i>	<i>pacifica</i>	4	132	35
							<i>Eurytemora</i>	spp. juveniles	35	6129	15
						Metridinidae	<i>Metridia</i>	<i>pacifica</i>	15	865	28
						Calanidae	<i>Neocalanus</i>	<i>flemingeri</i>	7	194	32
							<i>Mesocalanus</i>	<i>tenuicornis</i>	4	237	31
						Clausocalanidae	<i>Pseudocalanus</i>	<i>minutus</i>	113	175,895	3
							<i>Pseudocalanus</i>	<i>newmani</i>	98	50,573	9
							<i>Pseudocalanus</i>	spp. juveniles	121	489,773	1
						Scolecitrichidae	<i>Scolecithricella</i>	<i>minor</i>	81	29,798	10
						Tortanidae	<i>Tortanus</i>	<i>discaudatus</i>	28	1334	24
				Harpacticoida		—	—	—	26	1030	25
				Cyclopoida		Oithonidae	<i>Oithona</i>	spp.	109	140,703	4
				Poecilostomatoida		Oncaeidae	<i>Oncaea</i>	spp.	2	120	36
				Cladocera		Podonidae	<i>Podon</i>	<i>leuckartii</i>	52	2874	20
		Thecostraca	Cirripedia	—		—	—	—	103	56,914	7
		Malacostraca	Eumalacostraca	Amphipoda	Gammaridea	Lysianassidae	<i>Cyphocaris</i>	<i>challengeri</i>	6	68	38
					Hyperideia	Hyperidae	<i>Parathemisto</i>	<i>pacifica</i>	27	866	27
				Euphausiacea		Euphausiidae	—	—	43	6270	14
				Cumacea		—	—	—	5	74	37
				Decopoda		Crangonidae	—	—	1	10	41
						Hippolytidae	—	—	56	1801	22
						Pandalidae	—	—	8	137	34
						Majidae	—	—	63	4404	18
						Atelecyclidae	—	—	1	11	40
						Paguridae	—	—	15	415	30
Chordata	Tunicata	Appendicularia (Larvacea)		Copelata		Oikopleuridae	<i>Oikopleura</i>	spp.	95	58,479	6
Chaetognatha		Sagittoidea		Aphragmophora		Sagittidae	<i>Sagitta</i>	spp.	65	4685	17

## Appendix II

List of forage fish species and taxa collected from 1997 to 1999 in Lower Cook Inlet, Alaska. Sites: number of sites (101 possible) at which each group was collected; Number: estimated total number of individuals collected; and Rank: rank order of abundance. Groups shown are those used for analyses.

Family	Genus/Species	Common name	Sites	Number	Rank
Petromyzontidae	<i>Lampetra tridentata</i>	Pacific lamprey	11	16	16
Clupeidae	<i>Chupea pallasii</i>	Pacific herring	51	38,600	2
Osmeridae	<i>Mallotus villosus</i>	Capelin	30	4709	4
	<i>Spirinchus thaleichthys</i>	Longfin smelt	10	463	6
	<i>Thaleichthys pacificus</i>	Eulachon	2	2	30
Salmonidae	<i>Oncorhynchus gorbuscha</i>	Pink salmon	10	144	8
	<i>Oncorhynchus kisutch</i>	Silver salmon	1	4	22.5
	<i>Oncorhynchus nerka</i>	Red salmon	6	30	12
	<i>Oncorhynchus tshawytscha</i>	King salmon	18	119	9
Gadidae	<i>Gadus macrocephalus</i>	Pacific cod	37	1073	5
	<i>Theragra chalcogramma</i>	Walleye pollock	43	21,990	3
Gasterosteidae	<i>Gasterosteus aculeatus</i>	Threespine stickleback	2	2	30
Scorpaenidae	<i>Sebastes</i> spp.	Rockfish spp.	1	1	35.5
Hexagrammidae	<i>Hexagrammos stelleri</i>	Whitespotted greenling	2	4	22.5
	<i>Ophiodon elongatus</i>	Lingcod	2	29	13
Cottidae	<i>Radulinus asprellus</i>	Slim sculpin	1	2	30
	<i>Hemilepidotus papilio</i>	Butterfly sculpin	3	4	22.5
Hemitripterae	<i>Blepsias bilobus</i>	Crested sculpin	2	2	30
	<i>Hemitripterus villosus</i>	Shaggy sea raven	1	1	35.5
Psychrolutidae	<i>Psychrolutes paradoxus</i>	Tadpole sculpin	3	4	22.5
Agonidae	<i>Podothecus accipenserinus</i>	Sturgeon poacher	3	3	26.5
	<i>Pallasina barbata</i>	Tubenose poacher	1	1	35.5
	<i>Aspidophoroides monopterygius</i>	Alligatorfish	1	1	35.5
	<i>Anoplagonus inermis</i>	Smooth alligatorfish	1	1	35.5
Cyclopteridae		Lumpsucker spp.	4	10	18
	<i>Eumicrotremus orbis</i>	Pacific spiny lumpsucker	1	2	30
Bathymasteridae	<i>Bathymaster signatus</i>	Searcher	4	4	22.5
Zoarcidae	<i>Lycodes brevipes</i>	Shortfin eelpout	1	13	17
Stichaeidae	<i>Lumpenus</i> spp.		14	196	7
Zaproridae	<i>Zaprora silenus</i>	Prowfish	9	19	15
Trichodontidae	<i>Trichodon trichodon</i>	Pacific sandfish	14	111	10
Ammodytidae	<i>Ammodytes hexapterus</i>	Pacific sand lance	76	161,173	1
Pleuronectidae	<i>Atheresthes stomias</i>	Arrowtooth flounder	6	62	11
	<i>Hippoglossus stenolepis</i>	Pacific halibut	6	6	19
	<i>Hippoglossoides elassodon</i>	Flathead sole	3	4	22.5
	<i>Lepidopsetta polyxystra</i>	Northern rock sole	1	3	26.5
	<i>Platichthys stellatus</i>	Starry flounder	1	1	35.5
Sepiolidae	<i>Rossia pacifica</i>	N. Pacific bobtail squid	8	27	14

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